Stand dynamics of mixed-*Nothofagus* forest

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Abstract

Sustainable management of mixed-species forests for timber is underpinned by research on forest stand dynamics and quantification of tree recruitment, growth and mortality rates. Different performance among species across light gradients theoretically prevents more shade-tolerant species from excluding shade-intolerant species, driving succession and allowing species coexistence.

This research investigates stand dynamics and performance trade-offs for co-occurring tree species: *Nothofagus fusca* (red beech) and *Nothofagus menziesii* (silver beech), which together dominate extensive areas of New Zealand's indigenous forest. Using permanent plot data, measurements of permanently tagged individuals are used to quantify recruitment, growth and mortality rates for each species, across size classes and life-history stages (i.e. seedlings, trees). First, seedling growth and mortality is examined in relation to microhabitats (e.g., light, substrate type) and contrasted with patterns of seedling abundance. Second, spatially explicit permanent plot data are used to examine tree growth in relation to competition, local disturbance and tree size over a 23-year period. Third, the influence of competition and disturbance on tree mortality and spatial patterns of tree mortality are examined. Fourth, a simulation model for tree population dynamics is parameterised for mixed-*Nothofagus* forest and used to evaluate long term consequences of disturbances (e.g. alternate harvesting regimes) on structure and composition.

Small-scale disturbance favoured each species at different life stages and for different measures of performance (i.e. recruitment, growth or mortality). *N. fusca*

seedlings and trees grew fast in high light microhabitats, such as those created by small-scale disturbances, but adult *N. fusca* mortality was elevated near sites of recent disturbance. By contrast, *N. menziesii* trees grew faster near sites of recent disturbance, which may help this species persist. Consequently, simulation results showed that small-scale disturbance frequency was a major determinant of forest composition and structure, determining whether *N. fusca* or *N. menziesii* is dominant. The simulation model could be developed further and used to inform the sustainable management of mixed-*Nothofagus* forests.

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Chapter 1 Introduction

A large proportion of terrestrial biodiversity is harboured by forested ecosystems, with both direct and indirect values for humans (Millennium Ecosystem Assessment 2005). Direct values of forests include the provision of resources (e.g., timber, fibre, food and medicines) whilst indirectly forests assist in the maintenance of ecosystem functions (e.g., carbon sequestration, nutrient cycling, regulation of local or regional climate; Blaikie and Jeanrenaud, 1996; Foley et al., 2005). On a human-dominated planet, it is essential that biodiversity is sustained within forests that also meet human needs.

From an ecological perspective, sustainable forest management may include broad goals such as the maintenance of ecological diversity, functioning, protection of sensitive species or other ecological values (Coates and Burton, 1997). From a silvicultural perspective, sustainable forest management is often considered to be the perpetuation of a constant supply of timber or other resources (Puettmann et al., 2008). In order to directly assess the sustainability of any silvicultural system, field trials are required. Field trials can assess how aspects of the silvicultural system (e.g., harvest intensity and gap size, shape, density, location and orientation) influence understory microsite conditions, regeneration patterns and the growth and survival of residual trees (Coates and Burton, 1997). When field trial data are rare or unavailable, however, the stand dynamics of unmanaged forests can help to inform the sustainable management of forests.

Forest stand dynamics studies focus on changes in forest structure and composition through time, which are mainly driven by three demographic processes: recruitment, growth and mortality. As a consequence, stand dynamics studies frequently use permanent plot data that records the fate of individual trees. In mixed species forests, the different recruitment, growth or mortality rates of co-occurring species can be used to explain compositional or structural trends. The natural variability in forest structure that occurs within unmanaged stands can also be exploited to understand variation in recruitment, growth, and mortality of each component species across differing situations or gradients of interest (e.g., light, neighbourhood competition) (e.g., Coates, 2000; Canham et al., 2004). Silvicultural issues can then be addressed through the use of simulation models that incorporate the species-specific recruitment, growth and mortality rates (Thorpe et al., 2010; Kunstler et al., 2013). Simulation models are also essential because the potential life span of many tree species exceeds the length of most research studies; simulation models allow long term projections to be made from short term measurements.

Notwithstanding the long life span of most forest trees, relatively short-term observations can also provide a basis to understand the role of demographic processes for species coexistence. The different demographic rates of co-occurring species are considered to result in 'performance trade-offs', so that each species in a plant community can, on average, outperform each of the other species in some situation that may vary in time and space. Performance trade-offs are the result of fundamental fitness differences between species, and occur, for example, when the advantage of performing one ecological function well (e.g., utilising a certain resource) comes at the cost of

performing another function (e.g. consuming a different type of resource; Kneitel and Chase, 2004). In traditional niche theory, 'performance trade-offs' are a recognised requirement for species coexistence (Chesson, 2000, Kneitel and Chase, 2004). Shifts in the relative performance of species between different situations (e.g., microhabitats, competitive environments) result in 'rank-reversals' in average species performance: if the performance of each species in one situation is plotted against performance in another situation then a reversal in performance rank between species would occur (Kneitel and Chase, 2004; Baraloto et al., 2005). Though a vast array of life-history strategies may contribute to a tree species performance in any given environment (e.g., pollination strategies, seed production, seed dispersal), this thesis focuses on recruitment, growth and mortality rates as measures of performance. Performance trade-offs are broadly grouped as (a) trade-offs driven by different microhabitat preferences between species ('microhabitat trade-offs'), and (b) trade-offs that arise through rank reversals in performance through developmental stages ('ontogenetic trade-offs').

1.1 Microhabitat trade-offs

The different regeneration or successional niches and life-history strategies evident amongst species are considered central for understanding forest succession, dynamics and species coexistence (Grubb, 1977; Runkle, 1981; Denslow, 1985, 1987; Kobe et al., 1995). Recognition of the importance of disturbance as a driver of stand dynamics in temperate forests has given rise to the concept of 'patch dynamics' whereby disturbances create sites for tree recruitment (Pickett and White, 1985). Disturbances that result in canopy gaps are an important cause of spatial and temporal variability in light, which is recognized as a major limiting resource in forests (Pickett

and White, 1985; Oliver and Larson, 1990). Strong vertical and horizontal gradients in light availability in the understory can result in low light levels under closed canopy (e.g., 1–2% PAR), much less than that of tree-fall gaps (Canham et al., 1990). Other microclimatic and edaphic factors also vary between intact forest and canopy gaps, however light is usually considered the most important from a tree performance perspective.

The importance of successional niches for forest stand dynamics is often examined through considering juvenile demographic performance of coexisting species under differing light environments. In many temperate forests, for example, a performance trade-off among species is observed between species growth in high light, and survival in low light (Kobe et al., 1995; Kobe and Coates, 1997; Canham et al., 2006; Kneeshaw et al., 2006). Some studies have failed to find evidence of different successional niches of co-occurring species (Sipe and Bazzaz, 1995), however it is nevertheless generally accepted that the performance differences of juveniles amongst microhabitats play a key role in forest dynamics (Pacala et al., 1996; Rees et al., 2001).

1.2 Ontogenetic trade-offs

Adult tree growth and mortality rates are also fundamental to stand dynamics and can exert a dominant influence on forest structure and may determine population persistence (Muller-Landau et al., 2006). Nakashizuka (2001), in a highly cited paper, proposed that mechanisms of coexistence should differ through the developing stages of the life-history of trees. Coexistence could be promoted if the relative performance of tree species changed between developmental stages: poor performance by a species at

one life stage may be compensated for by better performance at another life stage (Nakashizuka, 2001; Silvertown, 2004). Such 'ontogenetic' performance trade-offs could emerge as the result of different age or size related performance among species in terms of one specific component of performance (e.g., growth), or amongst more than one fitness component across developmental stages (for example, differences in tree mortality or longevity may compensate for low seedling recruitment rate or low seedling survival (Lusk and Smith, 1998; Nishimura et al., 2009).

Ontogenetic trade-offs may be especially important for long-lived organisms such as trees, because demographic rates of tree species vary considerably across life stages or size classes. Furthermore, the relative importance of resource availability for tree growth or mortality rates can also change across developmental stages. Several studies have shown, for example, that rankings of species in terms of shade tolerance (i.e., the ability of plants to survive in low light) can vary with plant size (Kneeshaw et al., 2006; Kunstler et al., 2009). However, while numerous studies report demographic rates for tree species, these often focus on specific developmental stages, commonly seedlings or canopy trees above a certain size threshold, and less commonly consider patterns across a range of tree developmental stages (e.g., from small seedlings right through to canopy trees). Without understanding variation in demographic rates across developmental stages, there is the risk of developing a biased view of the role of trade-off strategies in forest dynamics and coexistence (Kneeshaw et al., 2006; Kunstler et al., 2009).

1.3 Study system

This research investigates performance trade-offs for two co-occurring closely related tree species: *Nothofagus fusca* (red beech) and *Nothofagus menziesii* (silver beech), which together dominate extensive areas of New Zealand's remaining indigenous forest. The ecology and dynamics of New Zealand's *Nothofagus* (southern beech) forests have been the subject of considerable previous research (see Wardle, 1984; Ogden et al., 1996). This has occurred because of the very distinctive character of New Zealand *Nothofagus* forests and their dominance across the New Zealand landscape. New Zealand's Southern beech, whether occurring as 'pure beech forest' or 'mixed beech forest' (i.e. admixtures of beech and other hardwood or Podocarp species) is considered temperate rainforest and is associated mainly with southern latitudes and mountainous regions (Wardle, 1984). This section provides an introduction to the ecology, dynamics and management of New Zealand *Nothofagus* forests, with a focus on mixed *Nothofagus fusca – N. menziesii* forest (hereafter 'mixed-*Nothofagus* forest'). Although members of the same genus and occurring in the same generic subsection (Quadripartitae), *N. fusca* and *N. menziesii* occur in different pollen groups (Hill and Read, 1991). The closest relatives of *N. menziesii* (menziesii-type pollen) are probably the Australian species *N. cunninghamii* and *N. moorei*, while the closest relatives of *N. fusca* (fusca-type pollen) are the New Zealand species *N. solandri* and *N. truncata* (Hill and Read, 1991).

Across New Zealand, *Nothofagus* distribution is characterised by major disjunctions and isolated outlying populations (Wardle, 1984; Ogden et al., 1996). Disjunctions in the present-day *Nothofagus* distribution are generally accepted to result

from slow spread of *Nothofagus* after the last glacial period, often compounded by locally unsuitable environmental conditions, although reasons for slow spread of *Nothofagus* are not clear (McGlone et al., 1996). The mixed-*Nothofagus* forests in which this research is conducted are similar to those that frequently occupy deep soils on fertile terraces and lower valley slopes in the North-Western South Island of New Zealand. This forest type is relatively simple, being dominated by just these two canopy species which appear to have maintained a long-term stable coexistence (McGlone et al., 1996).

In terms of basal area and live-stem biomass, *N. menziesii* and *N. fusca* are the most dominant tree species of New Zealand's remaining indigenous forest (Peltzer and Payton, 2006). Indeed, a recent vegetation survey and subsequent vegetation classification analysis revealed that at least 40% of New Zealand's remaining forest and scrub communities features one or both of these species as a major canopy dominant (Wiser and Hurst, 2008; Wiser et al., 2011). When just mature, tall or old growth forest is considered, the proportion of indigenous forest cover dominated by these species is even greater (e.g., 55–60%; Wardle, 1984; Wiser and Hurst, 2008). *N. menziesii* and *N. fusca* often co-occur and mixed-*Nothofagus* forest is a prevalent forest type in New Zealand.

Southern Hemisphere *Nothofagus* forest, like other temperate forest systems, are subject to a range of periodic natural disturbances which vary in frequency and severity. These include drought (Skipworth, 1981; Hosking and Kershaw, 1985; Jane and Green, 1986), wind-throw (Jane, 1985; Martin and Ogden, 2006), snow damage (Burrows, 1977), earthquake damage and landslides (Allen et al., 1999; Vittoz et al., 2001), and

severe insect outbreaks (Wardle and Allen, 1983), amongst others (see Wardle, 1984). Disturbance ranges from small scale (e.g., 1–4 trees; Stewart and Rose, 1990), to landscape scale events that cause dieback over large areas of forest; for example, insect outbreaks have been implicated in forest canopy dieback and elevated mortality rates in *Nothofagus* (Wardle and Allen, 1983; Hosking and Kershaw, 1985).

Recognition of the importance of disturbance and regeneration for *Nothofagus* forest stand dynamics has meant that these processes have received some of the most detailed research attention. This has been especially true for mixed-*Nothofagus* forests (e.g., Stewart, 1986; Stewart and Rose, 1990; Stewart et al., 1991; Runkle et al., 1995, 1997; Wiser et al., 2007). *N. fusca* is considered shade-intolerant compared with *N. menziesii* and in relatively undisturbed mixed *Nothofagus* forest *N. menziesii* dominates sub-canopy tiers. This observation kindled speculation that in the absence of major canopy disturbance, *N. menziesii* would replace *N. fusca* (Holloway, 1954; Wardle, 1984) and to the hypothesis that these species coexist by way of differing life history strategies, where *N. menziesii* has low juvenile mortality rates, and *N. fusca* has greater longevity and adult survival (Wardle, 1984). However, whilst small seedlings and saplings of relatively shade-tolerant *N. menziesii* are often common under closed forest, Stewart (1995) observed that even small *N. menziesii* seedlings (e.g., 5–15 cm) could become suppressed in low light and suggested that suppression may be a common cause of seedling mortality for both species. Despite this, seedling growth and mortality of *N. fusca* and *N. menziesii* have not yet been measured in forests where these species co-occur. Kunstler et al. (2009) measured seedling growth and mortality rates of *N. menziesii* in a lowland temperate forest and found relatively high mortality rates in low-

light, with most recruitment into larger size classes occurring due to fast low-light seedling growth, rather than low seedling mortality (Kunstler et al., 2009).

Rather than direct measurement of seedling growth and mortality rates, other studies have examined recruitment processes by measuring patterns of seedling and sapling density. Wiser et al. (2007) studied recruitment processes in canopy gaps formed by experimental coupe selection harvests in mixed *Nothofagus* forest and found that the relative density of *N. fusca* saplings six years after harvesting was greater in large rather than small canopy gaps created by the experimental harvest, whilst the opposite trend was apparent for *N. menziesii*. Nevertheless, the common co-occurrence of *N. fusca* and *N. menziesii* seedlings and saplings in gaps suggests that the two species may have considerable niche overlap, and reconstruction of disturbance history and size and age-class structures suggests that both species require canopy gaps for successful recruitment (Stewart and Rose, 1990).

Given that in the absence of any major canopy disturbance, both species regenerate via a gap-phase mode, it is interesting to consider how life-history differences at other life stages may contribute to species coexistence and stand dynamics of mixed-*Nothofagus* forests. In both species, seed dispersal is generally poor and accomplished by wind and gravity, and seeds are thought to lose viability rapidly in natural conditions (Wardle, 1984). In terms of differences at adult tree life stages, small *N. fusca* trees may attain faster growth rates than *N. menziesii* (reaching the canopy first even when the tree established many decades after the *N. menziesii*). However Runkle et al. (1997) concluded that small trees of both species could grow at similar rates for decades and that trees of both species could withstand periods of suppression. This

result may be a reflection of the methods employed because only growth rates of individuals that were still alive when the stands were sampled could be included in their dendrochronological study, which likely biases the sample of trees to those which were growing faster than average (Runkle et al., 1997). The study of Runkle et al. (1997) points to considerable overlap in diameter growth rates between *N. fusca* and *N. menziesii* and other studies have also shown beech growth varies considerably both within and between species (Wardle, 1984; Richardson et al., 2011). One reason why studies of beech growth rarely correspond with one another probably rests in the fact that growth is heavily influenced by the relative intactness of stands and their disturbance history (Wardle, 1984). For example, Allen et al. (2003) showed that most of the variation in individual tree growth rates could be explained by factors related to the individual tree or stand (e.g., tree diameter, crown size and neighbourhood basal area) rather than site factors (e.g., soil fertility). Wiser et al. (2005) also found only minimal influence of site factors on growth. Importantly, in the latter study, all residual *N. menziesii* trees on the edge of harvested small coupes (created as an experimental silvicultural treatment) exhibited compensatory marked growth responses, whilst only small *N. fusca* trees responded.

The studies cited above provide much detailed information on the stand dynamics of mixed-*Nothofagus* forests, but there has so far been a paucity of studies that document rates of recruitment, growth and mortality of *N. fusca* and *N menziesii*. For example, while juvenile life history differences are commonly cited as the key to understanding stand dynamics of mixed-*Nothofagus* forests, there is very little known about how fast seedlings or saplings of each species actually recruit, grow and die.

Seedling growth and mortality rates have not been measured previously in forests where these species co-occur. Previous studies on tree growth and mortality in mixed-*Nothofagus* forest have mostly used either stand reconstruction techniques (e.g., measuring growth of a surviving subpopulation of trees; Runkle et al., 1995, Runkle et al., 1997), or relatively small permanent plots (e.g., Wiser et al., 2005); by contrast, the use of large spatially mapped permanent plots (0.8–1 ha) with repeat measurements, provides capacity to relate growth and mortality to features of each individual tree's neighbourhood.

The primary objective of the research described in this thesis is to advance our understanding of stand dynamics in natural unmanaged mixed-*Nothofagus* forest, through examining the demographic processes of recruitment, growth and mortality. Specifically, this thesis aims to identify microhabitat and ontogenetic performance trade-offs between these species and to consider their role in stand dynamics. This involved periodic re-measurements of permanently tagged individuals to quantify rates of recruitment, growth and mortality for each species across a range of size classes and life-history stages (i.e. seedlings through to canopy trees). A secondary objective is to develop a simulation model of forest stand dynamics for mixed-*Nothofagus* forest that can be used to inform the sustainable management of these forests for timber production.

Following this introduction, this thesis comprises four data chapters. **Chapter 2** examines the performance of seedlings (<1.35 m tall) and involved the measurement of demographic rates (growth and mortality) of seedlings in relation to microhabitats (light and substrate type). Specifically, patterns of seedling abundance amongst microsites are

compared with ongoing performance in terms of seedling growth and mortality. **Chapter 3** examines the influence of neighbourhood competition and disturbance on tree growth rates. Using spatially explicit data collected over a 23-year period, individual-level growth of *Nothofagus fusca* and *Nothofagus menziesii* is analysed, to examine variation in growth across gradients of neighbourhood competition, local disturbance, and across tree sizes. **Chapter 4** examines the influences of neighbourhood competition and disturbance on tree mortality. Spatial point process analyses are undertaken to examine the spatial patterns of tree mortality for each species over a 23-year period. In the final data chapter (**Chapter 5**) a spatially explicit simulation model for tree population dynamics is presented, which is parameterised specifically for mixed-*Nothofagus* forest. This model uses the parameterised tree recruitment, growth and mortality patterns (i.e. described in Chapters 3 and 4) to evaluate the consequences of disturbances of varying frequency, on long term trends in forest structure and composition. The potential long term effects on forest composition and structure of two alternate harvesting regimes for mixed-*Nothofagus* forest are examined. The final chapter of the thesis (**Chapter 6**) provides a synthesis of the research results and discusses implications from this research for the sustainable management of mixed-*Nothofagus* forest.

Chapter 2 Seedling growth and mortality over three years across microsites in mixed-species *Nothofagus* forest

2.1 Introduction

Forest understories are a complex mosaic of differing microsites resulting from disturbance processes and gap creation (Harper, 1977; Christy and Mack, 1984; Pickett and White, 1985), with the establishment, growth and survival of tree seedlings depending on microsite conditions in their immediate vicinity (Grubb, 1977; Harper, 1977). The relative performance of seedlings of different species amongst different microsites drives forest dynamics and is also thought to promote species coexistence (Grubb, 1977; Silvertown, 2004). In the relatively shaded forest understories, light is widely considered the main microsite factor influencing tree seedling performance, although other factors such as soil properties can also be important.

For seedlings and saplings, studies have generally shown that the ability of species to survive in low light trades-off against the ability to grow quickly in high light (Pacala et al., 1994; Kobe et al., 1995; Kobe and Coates, 1997). Light-demanding species, for example, grow quickly in high light to capture canopy gaps, but tend to die if overtopped or shaded; shade-tolerant species in contrast have slower growth rates in high light, but are better able to survive in shaded forest understories. This growth-mortality trade-off can result in a 'rank-reversal' in the overall performance of species

along light gradients, ensuring that coexisting species each perform best in certain conditions and resulting in spatial or temporal segregation of species (i.e. niche partitioning; Nakashizuka 2001).

At a mechanistic level, the differing life history strategies displayed by shade-tolerant vs. intolerant species are the consequence of morphological, physiological and allocation constraints that influence light capture (Valladares and Niinemets, 2008): shade-tolerant species are usually characterised by tough, long-lived leaves and low specific leaf area (leaf area per unit mass); in contrast, shade-intolerant species typically have higher specific leaf area, higher assimilation rates and higher leaf area ratios (i.e. leaf area per unit plant mass; Valladares and Niinemets, 2008). Changes in biomass allocation or morphology with ontogeny can influence shade-tolerance and the relative performance of species (Kitajima, 1994; Lusk, 2004). Therefore, when examining the performance of seedlings across light gradients, plant size should also be taken into account (Kneeshaw et al., 2006; Kunstler et al., 2009). Greater or lesser resilience in shade-tolerant versus intolerant species to drought or herbivore attack, or other types of damage, can also influence size-related patterns of growth or mortality (Kitajima, 1994; Reich et al., 2003). Variation in plant performance across plant sizes can lead to 'ontogenetic' performance trade-offs, whereby co-occurring species are each able to perform better in some fitness component such as growth or survival, at a certain size-class or life stage (Baraloto et al., 2005).

As well as light, other microsite factors important for seedling establishment, growth and survival could provide further axes of variation along which demographic

performance trade-offs between species could arise. The understories of temperate forests comprise a mosaic of differing substrate types, including stumps, tip-up mounds, logs and pits (Christy and Mack, 1984; Christie and Armesto, 2003). It has commonly been observed that some types of substrate are more favourable for seedling establishment than others (June and Ogden, 1978; Gray and Spies, 1997; LePage et al., 2000). A higher density of seedlings growing on log substrates than on the ground in many temperate forests has led to the proposal that logs provide a 'safe-site' for seedling establishment (Takahashi et al., 2000; Lusk and Kelly, 2003; Vodde et al., 2011). Logs or other woody debris substrates may have elevated seedling establishment because seed adherence is more likely (Harmon, 1987), greater moss cover may provide a moister seedbed with reduced evapotranspiration (Iijima et al., 2006), and raised substrates such as woody debris may be less likely to accumulate a dense litter cover which can be detrimental to seedling establishment (Knapp and Smith, 1982; DeLong et al., 1997; Simard et al., 2003). While these factors may aid seeding germination and establishment, different conditions may favour the on-going growth and survival of seedlings into larger size classes (Takahashi et al., 2000; Iijima et al., 2007). Once a seedling has established, logs or other raised substrates offer sites of reduced competition with ferns and herbaceous plants (Christy and Mack, 1984; Harmon and Franklin, 1989; Coomes and Grubb, 2000), and increased nutrient availability may improve seedling performance (e.g., enhanced growth or reduced mortality; Coomes and Grubb 2000). Performance differences between species could also be further accentuated by any interacting effects of light and substrate microsites (Gray and Spies, 1997).

This study examines evidence for performance trade-offs between seedlings of two co-occurring species, *Nothofagus fusca* and *Nothofagus menziesii*, in old growth, mixed-species forest. For each species, patterns of naturally regenerated seedling density, growth and mortality are examined across microsites. Spatial patterns of seedling and sapling occurrence have been used previously to describe the regeneration niches of *N. fusca* and *N. menziesii* (e.g., Stewart and Rose, 1990), but here tagged individuals on repeat-measured plots are used to examine the demographic performance (i.e. growth and mortality rates) of seedlings of each species. *N. fusca* is considered to be shade-intolerant so is expected to have faster growth than shade-tolerant *N. menziesii* in high light, but higher mortality than *N. menziesii* in low light. Elevated microsites appear to be favourable for seedling establishment for both species, but particularly for *N. fusca* (Ogden, 1971; June and Ogden, 1975; Stewart and Rose, 1990). Little is known, however, about how seedling growth and mortality of these species varies across forest floor substrates (e.g., logs, tree stumps, mounds, etc.) so this is a key focus of this study. Small first-year *N. fusca* seedling survival appears to be higher on logs than on other substrates (June and Ogden, 1975) and it has previously been proposed that *N. fusca* seedling growth is also faster on raised substrates such as logs and tree stumps (Ogden, 1971; Stewart and Rose, 1990). I ask the following questions: 1) Is there a growth-mortality trade-off for shade intolerant *N. fusca* and shade tolerant *N. menziesii* amongst low-light and high-light microsites? 2) Do size-related growth or mortality patterns provide evidence for ontogenetic performance trade-offs (i.e. a rank reversal in performance across size classes) within the seedling life stage? 3) For each species, how do seedling density, growth and mortality vary across different forest floor

substrates? Evidence for ontogenetic performance trade-offs between the seedling life stage and tree life stage in these co-occurring species is further discussed in Chapter 6 ("*Synthesis and conclusions"*).

2.2 Methods

2.2.1 Species and study area

The study was conducted in low elevation old-growth broadleaved-evergreen forest in the Maruia Valley, South Island, New Zealand (42°13' S, 172°16' E). All three stands (Pell Stream, Rough Creek, Station Creek) were located on alluvial terraces and were dominated both in the canopy and in smaller size classes, by two species of southern beech: *Nothofagus fusca* (Hook. f.) Oerst. and *N. menziesii* (Hook. f.) Oerst. Together these species also co-dominate extensive areas of New Zealand forests and are two of the most dominant indigenous species in terms of basal are and stem density (Peltzer and Payton, 2006; Wiser et al., 2011). *N. fusca* is generally considered less shade tolerant than *N. menziesii* (Wardle, 1984), grows larger (up to 200 cm diameter, 30 m tall v. 150 cm diameter, 25 m tall for *N. menziesii*) and has shorter-lived leaves (1 year versus 3.5 years; Wardle, 1984). Elevation across the three study sites ranges from 450 to 600 m above sea level. Mean annual precipitation at nearby Springs Junction (425 m elevation, approximately equidistant to the three study plots) is 2280 mm, with >130 mm recorded every month (National Institute of Water and Atmospheric Research, unpublished data). Mean annual temperature is 9.8ºC, with a monthly

minimum of 3.8ºC (July) and monthly maximum of 15.2ºC (January). The studied stands all occur on terraces where the acidic soils (mineral soil pH 4.0) formed from alluvial sand and silt, overlying glacial outwash deposits with mixtures of granite, greywacke and schist (Bowen, 1964), and have relatively high levels of available P (Wiser, 2001).

2.2.2 Field methods

Seedling density

In 1986, systematically located seedling subplots were established at each of the three stands (Station Creek, Rough Creek, Pell Stream) to measure understorey vegetation composition and structure. These subplots were systematically placed along the tapes used to subdivide the 0.8–1.0 ha permanent plots, in a grid-like arrangement at 5 m spacing. In total, 361, 285 and 319 seedling subplots were established at the Station Creek, Rough Creek and Pell Stream stands respectively (differing number of subplots arise due to the different overall dimensions of the study plots). Each subplot was circular, with radius 0.3 m (area 0.09 m^2), in which all seedling species were identified and tree and shrub species were counted in height tiers (i.e., 0–15 cm, 15–45 cm, 45–75 cm, 75–105 cm, 105–135 cm). When cotyledon seedlings occurred, these were identified to genus if possible. The substrate type of each subplot was characterised as either ‘forest floor’, or ‘log’, ‘mound’, ‘stump’ or ‘pit’ (Stewart and Rose 1990). Seedling subplots were remeasured annually from 1987–1992. In November 1989,

additional systematic counts of *Nothofagus* cotyledons were made on each subplot. *Nothofagus* cotyledons were distinguished due to their distinctively shaped seed leaves, but could not however be identified to species level.

Seedling growth and mortality

In July 2009, 100 further seedling subplots (0.5–1.0 m^2) were randomly established (comprising 38, 30 and 32 subplots at the Station Creek, Pell Stream and Rough Creek plots respectively) on which *N. fusca* and *N. menziesii* seedlings were permanently marked in order to measure individual seedling growth and mortality rates. Following Stewart and Rose (1990), the predominant substrate of each subplot was characterised as 'forest floor', 'log' (>200 mm diameter), 'mound' (>30 cm raised above the general lay of the ground), or 'stump'. Log and stump substrates comprised coarse woody debris with either moderate or advanced decay following Stewart and Burrows (1994); bark was generally absent, and a knife blade could penetrate >2 cm. 'Pit' substrate types (Stewart and Rose, 1990) were not sampled as very few seedlings grew on these surfaces making sampling impractical. On each plot, sample points were randomly selected and located in the field; a subplot for each substrate type was then established on the nearest available site (where available) within 10 m of the random sample point. To aid efficiency of sampling, subplot locations were rejected if they had <10 seedlings, and the next closest substrate of that type, if present, selected. When subplot locations had >50 seedlings, a 0.5 m^2 subplot size was used, otherwise subplots were 1 m^2. Subplot corners and boundaries were permanently marked.

Within each subplot, seedlings of each species (5–135 cm tall) were tagged using uniquely numbered aluminium tags attached to the seedling stem using a plastic zip-tie. Each seedling stem was marked with white paint at ground level. Seedling diameter was measured directly above this mark by taking two orthogonal diameter readings using digital callipers. On each seedling the extended (i.e. pulled-up) height from the paint mark to the top of the apical bud was measured. To assist with relocating all tagged seedlings at subsequent remeasurements, the orthogonal *x* and *y* coordinate of each seedling was recorded. Seedling remeasurements were undertaken in July 2010, July 2011 and July 2012. Deer and goat browsing of seedlings is negligible in the study area; insect browse seldom occurred but was recorded if present.

At each of the subplots an index of light availability was calculated using hemispherical photographs. In July 2010 digital hemispherical photographs were taken at 1.35 m above the ground in the centre of each subplot, using a Nikon Coolpix digital camera fitted with a 180º hemispherical (fisheye) lens. Images were analysed using Gap Light Analyser V2 software (Frazer et al., 1999). Average light transmission was estimated over a growing season (October–March). Total photosynthetically active radiation (PAR) was calculated as the sum of direct and diffuse PAR and in this study was expressed as a percentage of total PAR at the sampled point (Frazer et al., 1999). A subset of images were analysed three times (by different software operators) to ensure that results were not unduly affected by different threshold specification between observers (i.e., the classification of pixels of the image into sky and non-sky classes; Frazer et al., 1999).

Soil (i.e. substrate) samples were collected from each of the 100 subplots in August 2011. These were collected using a hardened (heat-treated) 50 mm diameter steel soil-corer, fitted with a removable internal aluminium sleeve. The corer was able to be hit through relatively hard substrates with minimal disturbance of the substrate or soil compression. Between 3–5 samples were collected at each subplot, air-dried, homogenised, sieved and then subsampled for laboratory analysis to measure organic Phosphorous content (following Blakemore et al., 1987 and Lachat Instruments, 1998). To document the drying cycle of each subplot during fine spells of weather (because substrate types could be expected to dry at different rates) soil volumetric water content was also measured using a soil moisture meter on each subplot in February 2012. All subplots were sampled both three and five days following a heavy rainfall event, but subsequent rain precluded further measurements.

2.2.3 Data analysis

Seedling density

To examine the suitability of differing substrates for seedling establishment the density of cotyledonary seedlings was examined across different substrate types. Cotyledon count data was analysed using a generalised linear model with a logarithmic link and a negative binomial error distribution, to account for the zero-inflated and over dispersed data (Crawley, 2007). The *Nothofagus* cotyledons could not be identified to species level so this analysis was undertaken for both species combined. A full model

that included substrate type and plot was compared to reduced models using likelihood ratio tests, to obtain Chi-square statistics for each of these factors. To examine differences in the density of established seedlings (0–135 cm tall, excluding cotyledons) across different substrate types (updating analyses undertaken by Stewart and Rose, 1990), the 1986–1992 seedling count data were analysed in a similar way, separately for each species. Differences amongst plots and across years were accounted for by including plot and year as fixed factors. Full models were again compared to reduced models using likelihood ratio tests to obtain Chi-square statistics for each fixed effect. Results for the most supported model are presented for each species. Significant differences in seedling density amongst substrate types are reported for each species.

Seedling growth and mortality

For each species, the importance of light, substrate type and seedling size on seedling growth or mortality was assessed through comparing a set of models fitted to the data. The explanatory variables used comprised 1) initial seedling height (cm) to represent size-related ontogenetic effects: plant growth is usually strongly related to size; and 2) variables to represent competition for light or other resources: total PAR, substrate type, substrate organic Phosphorous content, relative seedling density; and 3) recent growth rate (cm y^{-1}; included in the mortality analyses only). The index to represent relative seedling density was calculated by determining the residuals of a power function fitted between density of seedlings (of both species; stems per 1 × 1m subplot) and mean seedling height (height, in cm): Small (negative) coefficients for

relative seedling density indicate that density is low relative to mean height of neighbouring seedlings, and vice versa. This approach was taken because seedling density could be expected to decline with increasing mean seedling height due to various sources of mortality. Although each seedling subplot typically sampled seedlings of a range of sizes, in general what could be regarded as dense for a subplot with relatively large seedlings (on average) may not be dense for a subplot with relatively small seedlings.

Absolute growth rates were analysed using non-linear models (Paine et al., 2012) in preference to rescaling seedling growth by initial seedling height to allow analysis with linear mixed models of relative growth rate (RGR). This was done because analyses of RGR can be subject to residual bias against size, if size effects on the absolute growth rate are not proportionate (e.g., see MacFarlane and Kobe 2006).

The absolute height increment (growth) of each seedling was calculated based on the first (June 2009) and last (July 2012) seedling measurement, then annualised to calculate a mean annual growth rate (cm y^{-1}). A non-linear, four-parameter Gompertz function was used to model the relationship between seedling growth (G, cm y^{-1}) and seedling height (in 2009; cm). This function takes the form:

$$G = \beta_1 + \beta_2 \times \exp(-\exp\ \beta_3 - \beta_4 \times height\ ) \qquad (1)$$

where $\beta_1 - \beta_4$ are parameters estimated by the analysis. The shape of this curve is highly flexible in modelling a positive relationship between seedling growth and height. In this function parameter β_1 shifts the curve along the *y*-axis; the function is asymptotic

at $G = \beta_2$; parameters β_3 and β_4 control the shape of the curve, with β_3 shifting the curve sideways along the *x*-axis and parameter β_4 controlling the upper inflection (see Anon, 1994). This function can be modified to allow the form of the relationship between growth and initial height to vary with other explanatory variables of interest. Because there were a number of potentially important explanatory variables it was impractical to fit models comprising all possible combinations of variables and possible functional forms. Instead, the following approach was taken to identify the most important explanatory variables. First, explanatory variables were each included into the function (equation 1) as simple additive effects. These models were compared to the 'height-only' model (equation 1), to assess the overall importance of each variable. This initial set of candidate models (6 models, Table 2.1) revealed that seedling growth of both *N. menziesii* and *N. fusca* was most strongly related to total PAR, while *N. fusca* seedling growth was also influenced by organic P and substrate type. A set of further models were then fit to examine whether modifying the asymptote and shape parameters (parameters $\beta_2 - \beta_4$ in equation 1) by these explanatory variables resulted in a better supported model.

Seedling growth models were fit using the `nlme` package in R (Pinheiro et al., 2013). Seedling growth data was normally distributed, but there was substantial variation in mean annual growth across all initial seedling height values. Initial exploratory analyses showed that there was greater variation in growth across seedlings with taller rather than shorter initial seedling height (see Appendix 2.1, Figure 2.4), so heteroscedasticity (variance increasing with the mean) was incorporated into the models. Finally, data sets that lack independence between observations such as that of

this study (i.e., seedlings were grouped within subplots and subplots were grouped within plots) violate the assumptions of ordinary least-squares regression and compromise statistical inference (Pinheiro and Bates, 2000). Seedlings growing on the same plot or subplot are likely to be subject to a range of similar, yet unmeasured, factors that could affect growth. A multilevel (i.e., mixed) modelling approach was used to allow for the incorporation of group-level predictors (e.g. inclusion of 'random' plot and subplot effects; Pinheiro and Bates 2000).

Models of individual-seedling mortality were constructed to parameterise the probability of seedling mortality in relation to the explanatory variables. These analyses were restricted to seedling deaths that occurred during the 2010–2012 period, so that recent growth over the earlier period (i.e., 2009–2010) could be used as an explanatory variable. The response variable is a vector indicating whether or not a seedling died over the 2010–2012 period (dead in 2012=1, alive in 2012=0). The probability of seedling mortality (P_m) was modelled using a generalized linear mixed model with a binomial error distribution for the response variable and a logit link (Crawley, 2007). As was done for the seedling growth analyses, these models accounted for two levels of random effects (i.e., subplots nested within plots). All mortality analyses were carried out in the statistical program R (R Core Team, 2012) using the `lme4` library (Bates et al., 2012). Results reported graphically are shown in terms of annual mortality rate (i.e., mortality rate=$1–(1–P_m)^{1/t}$; where t is the length of the mortality census period, in years). To ensure that the mortality regressions were not influenced by colinearity amongst the explanatory variables (e.g., recent growth and initial height) the Variance Inflation Factor (VIF) was calculated for the models that included both variables. VIF

was always <1.1 for both species, well below the threshold at which colinearity is likely to be present (e.g., VIF > 3.0; Zuur et al., 2010).

Model comparison using AIC

For both the seedling growth and seedling mortality analyses, support for each model was examined relative to others using the small sample version of Akaike's Information Criterion (AIC) and the associated 'Akaike weights' (w_i). AIC works by balancing goodness of fit versus the number of parameters included in a model, where models with the smallest AIC values are those most strongly supported by the data (Burnham and Anderson, 2002). Parsimonious models are favoured over more complex models (i.e., those with more estimated parameters) when $\Delta\text{AIC} \leq 2$. Each Akaike weight, w_i, describes the probability, given the data, of each model being the best in the candidate model set. For each species, the maximum likelihood parameter estimates from the most supported growth and mortality models were used to graph growth or mortality in relation to explanatory variables.

2.3 Results

2.3.1 Seedling occurrence across substrates

Over all plots combined, the most available substrate type for seedling establishment was ground substrate (76%), followed by logs (11%), mounds (6%), stumps (4%) and pits (3%). The density of cotyledons (both species combined) varied significantly across substrate types (X^2=28.6, P<0.001) and was highest on stumps and logs, intermediate on mounds, and least on ground and pit substrate types. Established seedling density varied across species, being three-fold greater for *N. fusca* than for *N. menziesii*. The density of established *N. fusca* seedlings varied across substrate types (X^2=33.6, P<0.001) and was higher on logs (P<0.001) and stumps (P<0.001) than expected based on the frequency of these substrate types (e.g., 24% and 16% of total seedlings occurred on logs and stumps respectively, but these comprised only 11% and 4% of available substrates). Density of established *N. menziesii* seedlings also varied across substrate types (X^2=49.7, P<0.001) with overall more seedlings located on mounds (P=0.009) and logs (P=0.014) than expected (e.g., 25% and 19% of total seedlings occurred on mounds and logs respectively, which comprised only 6% and 11% of available substrates).

Substrate moisture content five days after a heavy rain event was highest on average for logs (43% ± 18 sd), followed by forest floor (37% ± 16 sd), stumps (33% ± 11 sd) and mounds (25% ± 6 sd). Following heavy rainfall, there was minimal drying on average of all substrate types after 3–5 days of fine weather.

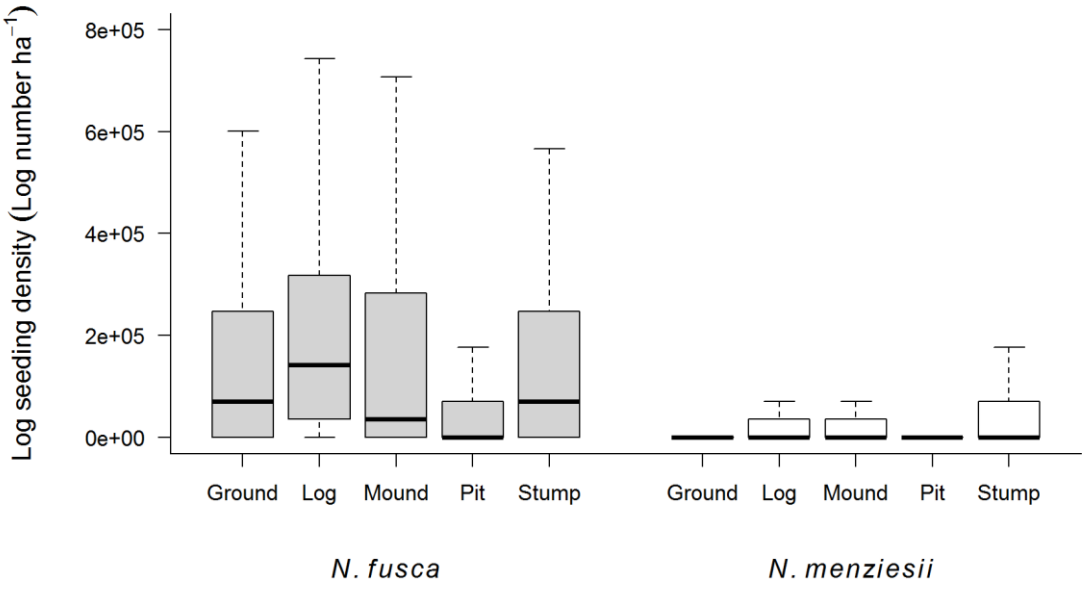

Figure 2.1. Boxplot of established seedling (0–135 cm tall) density (log number ha^{-1}) of *N. fusca* and *N. menziesii* growing on 'ground', 'log', 'mound', 'pit' and 'stump' substrates. Outliers are not shown.

2.3.2 Seedling growth

The mean initial size of the tagged seedlings sampled was similar for both species and was 1.8 ± 0.02 SEM (standard error of the mean) mm in diameter and 33.2 ± 0.7 SEM cm in height for *N. fusca*, and 2.3 ± 0.07 SEM mm in diameter and 35.4 ± 1.3 SEM cm in height for *N. menziesii*. The overall mean absolute height growth rate was 2.2 ± 0.1 SEM cm year^{-1} for *N. fusca* and 2.8 ± 0.2 SEM cm year^{-1} for *N. menziesii*.

Total PAR was the most important explanatory variable for seedling growth and for both species substantially reduced the AIC compared to the 'height-only' model (e.g., by 12.2 units for *N. fusca* and 11.9 units for *N. menziesii*; Table 2.1). Height growth rate increased with increasing total PAR for both species (i.e. as indicated by positive coefficients, Appendix 2.1, Table 2.4). In general, in relatively high light (e.g., 20% total PAR) *N. fusca* seedlings of most sizes grew faster on average than *N. menziesii* (e.g., on ground, mound and stump substrate types, but not on logs; Figure 2.2c). By contrast, under low light conditions, *N. menziesii* seedlings of most sizes generally grew faster than *N. fusca* seedlings (Figure 2.2a).

Growth of both species increased substantially with seedling size (Appendix 2.1, Figure 2.4), but more so at relatively high light (Figure 2.2c): at low light size-related trends in height growth were minimal, especially for *N. fusca* (Figure 2.2a). These size related patterns in growth, combined with the light-related patterns in growth, meant that *N. fusca* did not always grow faster at moderate or high light than *N. menziesii*, in contrast to the general trend described above. For example small (e.g. < 30 cm) seedlings of *N. menziesii* grew faster at moderate to high light (apart from on stumps) than small *N. fusca* (e.g., a 20 cm tall *N. menziesii* on average grew 3.6 cm y^{-1} at 20% total PAR, compared with 1.7–2.6 cm y^{-1} for similarly sized *N. fusca* on ground, log and mound substrates; Figure 2.2c).

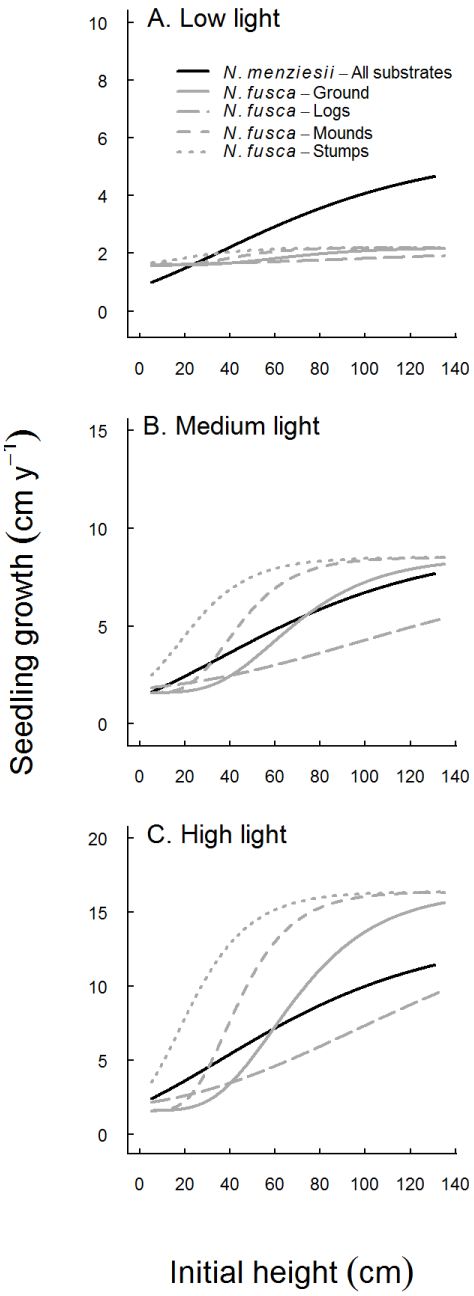

Figure 2.2. Mean annual seedling growth (cm y^{-1}) versus initial seedling height (cm) under (a) Low light (2% total PAR), (b) Medium light (10% total PAR) and (c) High light (20% total PAR), for *N. menziesii* (black line), and *N. fusca* growing on different forest floor substrates (grey lines). See panel A for key. Relationships are based upon the best supported model for each species (see Table 2.2). Note the different *y*-axis scales.

Table 2.1. Akaike's Information Criterion (AIC) statistics for initial seedling growth models, fit to *N. fusca* (n=1578) and *N. menziesii* (n=485) over the 2009–2012 period. Models were fit using non-linear mixed effect regression. The 'null' model fits the average seedling growth rate (cm y^{-1}), and the 'height only' model fits the relationship between seedling growth and height (cm) using a Gompertz function (see equation 1, methods). Other models are based on the height only model, with the additional variable included as an additive term. *K* is the number of fixed-effect parameters estimated in each model. ΔAIC is the difference in AIC between each model and the model with the lowest AIC. Parsimonious models (i.e. those with fewer estimated parameters) are favoured over more complex models when $\Delta AIC \leq 2$. Model weights (w_i) indicate the probability of each model being the best in the set.

Species	Variable	*K*	AIC	ΔAIC	w_i
N. fusca	Height + total PAR	5	7851.5	0	0.883
	Height + organic P	5	7856.6	5.0	0.071
	Height + substrate type	7	7857.7	6.2	0.040
	Height + relative seedling density	5	7862.7	11.2	0.003
	Height only	4	7863.7	12.2	0.002
	Null	1	7987.8	136.3	<0.001
N. menziesii	Height + total PAR	5	2320.2	0	0.986
	Height + organic P	5	2330.1	9.9	0.007
	Height + relative seedling density	5	2331.4	11.2	0.004
	Height only	4	2332.1	11.9	0.003
	Height + substrate type	7	2336.5	16.3	<0.001
	Null	1	2377.4	57.2	<0.001

Table 2.2. Akaike's Information Criterion (AIC) statistics for the final candidate models fit to *N. fusca* (n=1578) and *N. menziesii* (n=485) seedling growth over the 2009–2012 period. Models were fit using non-linear mixed effect regression, and only include the important explanatory variables previously identified (see Table 2.1). For each species, models are compared to a model which fits the relationship between seedling growth (cm y^{-1}) and height (cm) using a Gompertz function (see equation 1, methods). The asymptote (β_2) and shape parameters (β_3 and β_4) of this function are modified by the listed variables. *K* is the number of fixed-effect parameters in each model. ΔAIC is the difference in AIC between each model and the model with the lowest AIC in the candidate set. Parsimonious models (i.e. those with fewer estimated parameters) are favoured over more complex models when $\Delta AIC \leq 2$. Model weights (w_i) indicate the probability of each model being the best in the candidate set. The models used for subsequently graphing the effects of explanatory variables are highlighted in bold type.

Species	Model form	*K*	AIC	ΔAIC	w_i
N. fusca	**Total PAR and organic P modify β_2, substrate type modifies β_3 and β_4**	**12**	**7749.4**	**0**	**0.936**
	Total PAR modifies β_2, substrate type modifies β_3 and β_4	11	7755.4	6.0	0.046
	Total PAR and organic P modifies β_2, substrate type modifies β_3	9	7757.2	7.8	0.019
	Total PAR modifies β_2, substrate type modifies shape β_3	9	7772.7	23.3	0
	Total PAR and organic P modify β_2, substrate type modifies β_4	9	7773.3	23.9	0
	Total PAR modifies β_2, substrate type modifies β_4	8	7782.3	32.9	0
	Total PAR modifies β_2	5	7820.9	71.5	0
	Org P modifies β_2	5	7837.4	88.0	0
	Substrate type modifies β_3	7	7838.8	89.4	0
	Substrate type modifies β_4	7	7844.0	94.6	0
	Height + total PAR (i.e. total PAR included as an additive effect, see Table 3.1)	5	7851.5	102.1	0
N. menziesii	**Total PAR modifies β_2**	**5**	**2318.8**	**0**	**0.481**
	Height + total PAR (i.e. total PAR included as an additive effect, see Table 2.1)	5	2320.2	1.5	0.232

For *N. fusca*, growth varied substantially across substrate types; including substrate type in the growth model reduced the AIC compared to the 'height-only' model (e.g., by 6 units; Table 2.1). *N. fusca* growth was generally fastest on stump and mound substrates, intermediate on ground substrates and slowest on logs (e.g., see Figure 2.2b). Size-related growth patterns varied substantially amongst substrate types for *N. fusca* (Figure 2.2), especially at moderate-high light levels where differences amongst different substrate types were most marked for relatively large *N. fusca* seedlings (Figure 2.2b and c). For example, growth of relatively large (e.g., 100 cm height) *N. fusca* varied approximately 2-fold across substrate types, and under moderate light (e.g., 10% total PAR) was fastest on stumps (8.4 cm year $^{-1}$) and slowest on logs (4.3 cm year^{-1}, Figure 2.2b). Substrate type was unimportant for *N. menziesii* growth, as a model including substrate type received a higher AIC than a more parsimonious model (i.e. the 'height only' model; Table 2.1).

N. fusca seedling growth also varied with substrate organic P concentration (Table 2.1); unexpectedly, seedlings growing at sites with high organic P had slower growth than those at sites with low organic P (Appendix 2.1, Table 2.4). This result however is likely due to confounding effects between organic P and substrate type: logs tended to have high organic P, but seedlings on logs had considerably slower seedling growth than those on other substrates, as described above. For both species, seedling growth was unrelated to seedling relative density (Table 2.1).

2.3.3 Seedling mortality

The annual seedling mortality rate was highest for *N. fusca* at 0.044 deaths seedling^{-1} year^{-1} (138 out of 1606 seedlings died) versus 0.015 deaths seedling^{-1} year^{-1} for *N. menziesii* (15 out of 509 seedlings died). *N. fusca* seedling mortality was dependent on initial seedling height and recent growth rate, as the model that included both of these variables substantially reduced the AIC (i.e. by more than 24 units compared to the null model) and was the most supported model overall (Table 2.3). However, there was considerable model selection uncertainty, with the model including only initial seedling height performing almost as well (i.e. ΔAIC=2.1; Table 2.3), indicating that recent growth was relatively weakly correlated with *N. fusca* mortality. Mortality of *N. fusca* declined with increasing initial seedling height and with increasing recent growth rate (Figure 2.3). *N. fusca* mortality was unrelated to any other explanatory variable (i.e. total PAR, relative seedling density, substrate type or organic P). By contrast, for *N. menziesii* neither initial height nor recent growth nor any other tested explanatory variables were important predictors of mortality, since the null model received a lower AIC than all other models (Table 2.3).

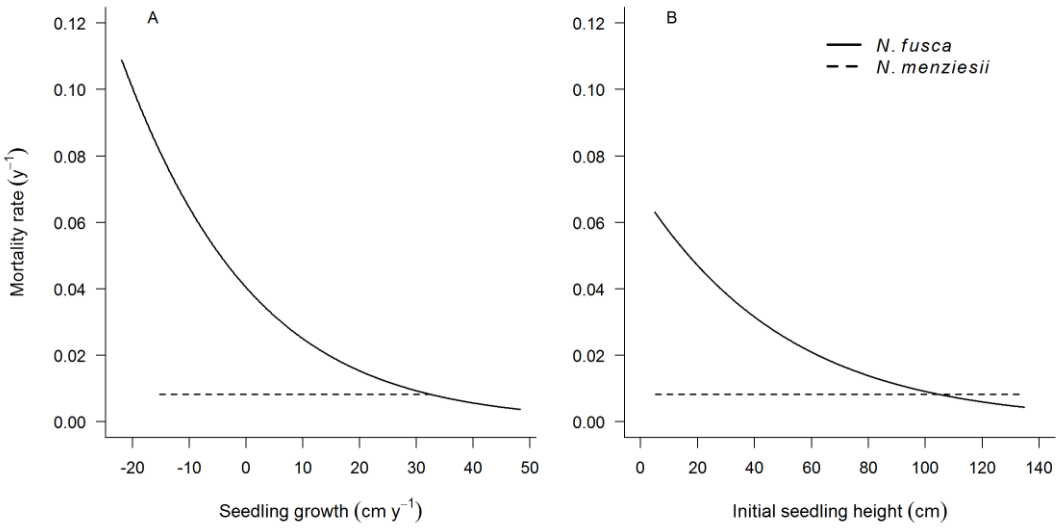

Figure 2.3. Mean annual mortality of *N. fusca* (solid lines) and *N. menziesii* (dashed lines), in relation to (A) seedling growth (cm y^{-1}); and (B) initial seedling size (cm). For *N. fusca*, lines are fit using the best supported individual based regression (see Table 2.3). For *N. menziesii*, mortality was unrelated to both seedling growth and initial height, so lines show the overall mean mortality rate.

Table 2.3. Akaike's Information Criterion (AIC) statistics for mortality models fit to *N. fusca* (n=1606) and *N. menziesii* (n=509) over the 2010–2012 period. Models fit the probability of seedling mortality using generalised linear mixed models. For each species, models are compared to the null model which fits the overall mean mortality probability. *K* is the number of fixed-effect parameters in each model. ΔAIC is the difference in AIC between each model and the model with the lowest AIC. Parsimonious models (i.e. those with fewer estimated parameters) are favoured over more complex models when $\Delta AIC \leq 2$. Model weights (w_i) indicate the probability of each model being the best in the candidate set. Models used for graphing effects of explanatory variables are highlighted in bold type.

Species	Model	*K*	AIC	ΔAIC	w_i
N. fusca	**Recent growth + initial height**	**3**	**867.6**	**0**	**0.736**
	Initial height	2	869.6	2.1	0.264
	Recent growth	2	884.3	16.7	0
	Null	1	891.7	24.2	0
	Total PAR	2	892.6	25.0	0
	Seedling relative density	2	892.9	25.4	0
	Organic P	2	893.1	25.6	0
	Substrate type	4	893.8	26.2	0
N. menziesii	**Null**	**1**	**136.4**	**0**	**0.258**
	Seedling relative density	2	137.0	0.6	0.196
	Initial height	2	137.6	1.1	0.144
	Organic P	2	138.2	1.8	0.104
	Total PAR	2	138.3	1.8	0.103
	Recent growth	2	138.3	1.9	0.102
	Recent growth + initial height	3	139.1	2.7	0.067
	Substrate type	4	141.1	4.7	0.025

2.4 Discussion

2.4.1 Growth and mortality trade-offs

Niche differentiation along light gradients is considered to be an important coexistence mechanism in forest communities (Grubb, 1977; Denslow, 1987). In mixed-*Nothofagus* forests, coexistence of *N. fusca* and *N. menziesii* has long been hypothesised to result from different species performance across light gradients due to differences in shade-tolerance, coupled with disturbance processes (Ogden, 1985, 1988; Stewart and Rose, 1990; Runkle et al., 1995). Previous studies documenting the abundance and growth rates of small *N. fusca* and *N. menziesii* in canopy gaps have demonstrated however that these species have considerable niche overlap at seedling, sapling and tree life stages (Stewart and Rose, 1990; Runkle et al., 1997). Because the seedling life stage is critical to forest development, it is surprising that seedling growth and mortality rates have not previously been measured in forests where these species co-occur. Growth of both species was faster in high-light, with total PAR the single most important explanatory variable explaining seedling growth. The finding that, in general, *N. menziesii* seedlings grew faster at relatively low light, while *N. fusca* seedlings grew faster at high light, confirms the long held assumptions regarding the growth performance of *N. fusca* and *N. menziesii* seedlings (Wardle, 1984).

Despite the importance of light for seedling growth, total PAR did not influence mortality of either species. For the shade-intolerant *N. fusca* seedling mortality was only weakly related to recent growth rate, while mortality of *N. menziesii* was unrelated to growth, which is indicative of a higher tolerance of slow growth in this species. Because

of a lack of a significant effect of light on mortality, these results provide only partial evidence for a growth-mortality trade-off between *N. fusca* and *N. menziesii* across light environments. The influence of light on mortality may be relatively weak for small seedlings, compared with other potential causes of seedling mortality, and it is to be expected that some seedling mortality is stochastic and likely to be driven by chance events (e.g., drought or physical damage from windfall debris) rather than light conditions. Furthermore, since relatively few seedlings of either species died over the three year study, a longer monitoring period may be necessary to better understand the influence of light or other factors on seedling mortality. Future work should examine whether growth-mortality trade-offs for these species become apparent at sapling life stages, or even whether they occur amongst seedling and sapling life stages (e.g., Kunstler et al., 2009).

2.4.2 Ontogenetic performance trade-offs

Ontogenetic performance trade-offs arise through rank reversals in species performance across size-classes or developmental stages (Baraloto et al., 2005). This study found some evidence of ontogenetic performance trade-offs between *N. fusca* and *N. menziesii*: growth of both species varied substantially across seedling sizes and rank-reversals in growth were observed between small vs. large *N. fusca* and *N. menziesii* seedlings, though this depended on the forest-floor substrate considered. Ontogenetic performance trade-offs have been previously shown in studies of seedling performance (Baraloto et al., 2005; Pérez-Ramos et al., 2012), as well as within sapling and tree life

stages (Clark and Clark, 1992; Sánchez-Gómez et al., 2008; Boyden et al., 2009) however ontogenetic trade-offs could also arise through performance differences across these drastically different life stages. Studies of plant performance conducted across only a limited life stage or span of plant sizes therefore have limitations. To evaluate the relevance of ontogenetic performance trade-offs for community structure and dynamics, studies conducted across a range of life stages are needed (Clark and Clark, 1992).

2.4.3 Differences in establishment, growth and mortality across substrates

Patterns of established seedling density are the net result of filters acting on seed dispersal, seed germination, and early survival (Harper, 1977; Schupp, 1995). Patterns of seedling density found in the present study indicate logs and stumps are important substrates for *N. fusca* and *N. menziesii* seedling establishment in mixed-*Nothofagus* forest. Total coarse woody debris biomass in the study area forests is unusually high compared to other New Zealand forest types (e.g., 130 vs. 54 Mg ha^{-1}; Stewart and Burrows, 1994; Richardson et al., 2009), though the actual area of log and stump substrates available for seedling establishment appears comparable to that in other New Zealand forest (e.g., logs occupied 11% of the total forest floor area of the study area forests cf. 9% in montane South Island forest; Bellingham and Richardson 2006) as well as overseas temperate forests (e.g., Christy and Mack, 1984). These coarse woody debris substrates harboured a disproportionate number of the pool of regenerating seedlings of both species, in agreement with previous studies showing seedling density

of both species is higher on elevated microsites (June and Ogden, 1975; Stewart and Rose, 1990). The significance of logs for establishment of seedlings has been previously ascribed to many factors including reduced competition with herbaceous vegetation (Harmon and Franklin, 1989), the facilitation of root anchorage provided by soft log substrates (DeLong et al., 1997), and the often high moss cover and greater moisture of log substrates (Duchesneau and Morin, 1999; Iijima et al., 2006), and increased likelihood of mycorrhizal inoculation (Tedersoo et al., 2008). Furthermore, *Nothofagus* spp. are relatively small seeded trees, so elevated substrate types may be particularly favoured for establishment as they don't accumulate deep litter layers that can impede establishment (Christy and Mack, 1984; Lusk and Kelly, 2003). Similar associations between seedlings and coarse woody debris substrates have been observed for other *Nothofagus* species, for example *N. nitida* seedlings of all sizes in southern Chile occur in greater density on log and stump substrates than on the ground, where woody substrates are also are assumed to play an important role in tree recruitment (Lusk, 1995). Conversely, that cotyledon and established seedling density of both species were least on ground and pit substrates may indicate impediments to establishment on these substrates. Water logging in pits is likely to be detrimental to establishment, as is the generally thicker litter layer on pit and ground substrates that may impede colonisation (Vodde et al., 2011).

A key finding of this study is that the favourability of logs as establishment microsites for both *N. fusca* and *N. menziesii* was not reflected in on-going patterns of growth and mortality. Despite seedlings of *N. fusca* being particularly abundant on logs, the growth analyses in the present study showed that seedlings of most sizes grew

considerably more slowly on logs than on other substrate types. This result indicates a shift in the favourability of logs for seedlings with increasing seedling size. Furthermore, for *N. fusca* the result appears to conflict with the findings of Ogden (1971) who showed that *N. fusca* seedlings of all sizes were associated with log substrates and that seedlings on logs were on average taller than those on other substrates (Ogden, 1971). *N. fusca* seedlings grew at high density on logs compared with other substrates, so one possible reason for slower growth on logs is that seedlings contend with increased competition with other seedlings. This is unlikely however to explain slower growth of large seedlings on logs in the present study because seedling growth was unrelated to relative seedling density. While below-ground competition for resources is likely to be lower on log substrates than on the ground, logs do not necessarily provide a higher nutrient microsite for seedlings. At the study sites, both carbon and nitrogen content increase and the C:N ratio declines during *Nothofagus* log decay (Stewart and Burrows, 1994). The decay of poor-quality litter such as coarse woody debris is known, however, to have dramatic effects on plant productivity: nitrogen is immobilised by microbial action drawing upon available forms of nitrogen, reducing availability to plants (Zimmerman et al., 1995). Alternatively, log substrates may provide insufficient water to large *N. fusca* seedlings, particularly in the driest summer months. Further investigation is required to determine the effects of summer drought on seedling growth and mortality on logs, and such work could include experiments that manipulate water as well as detailed work on the water status of decaying logs (e.g., Iijima et al., 2006).

2.4.4 Conclusion

Overall, this study provides some evidence for niche partitioning amongst these closely related co-occurring species, due to rank-reversals in the growth performance of *N. fusca* and *N. menziesii* across light gradients, amongst forest floor substrate types and across seedling sizes. Interactions amongst these factors also lead additional rank-reversals in performance, so that each species performed best under certain conditions. This study highlights the need to understand how seedling performance on forest floor microsites varies across developmental stages, for example at germination, establishment, and post-establishment phases, because the most favourable sites at one stage may not be the most favourable at later life-stages (Schupp, 1995).

Appendix 2.1

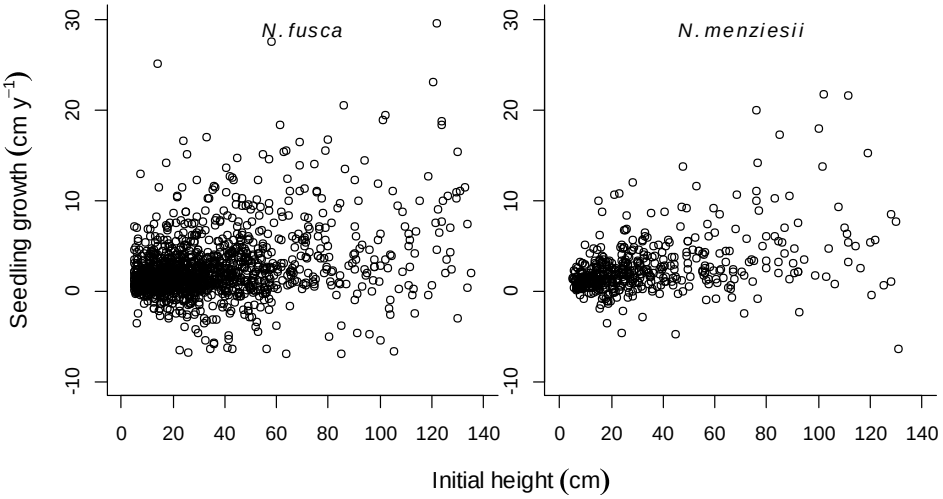

Figure 2.4. Distribution of seedling growth vs. initial seedling size, for *N. fusca* (n=1578) and *N. menziesii* (n=485).

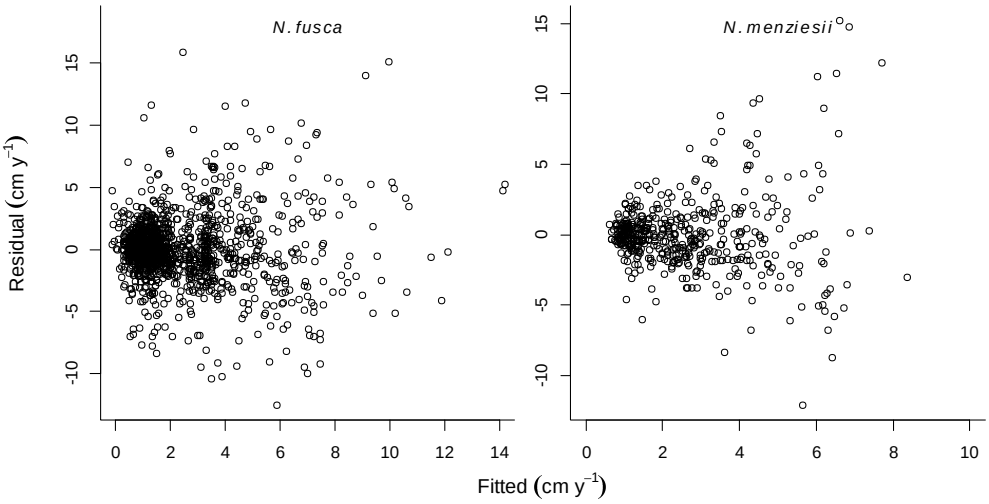

Figure 2.5. Residuals (observed–fitted) vs. fitted growth (cm y^{-1}), for the best supported individual-level seedling growth models, for *N. fusca* (n=1578) and *N. menziesii* (n=485).

Table 2.4. Maximum likelihood parameter estimates and standard error for the most supported individual-based seedling growth models (see Table 2.2, main text) for *N. fusca* and *N. menziesii* over the 2009–2012 period. The final models took the form:

for N. menziesii:

$$\text{Growth} = \beta_1 + \beta_2 + b_1.\text{total PAR} \times \exp - \exp \beta_3 - \beta_4.\text{height}$$

and for N. fusca:

$$\text{Growth} = \beta_1 + \beta_2 + b_1.\text{total PAR} + b_2.\text{organic P} .\exp - \exp \beta_3 + b_3.\text{sub}_{\text{log}} + b_4.\text{sub}_{\text{mound}} + b_5.\text{sub}_{\text{stump}} - \beta_4 + b_6.\text{sub}_{\text{log}} + b_7.\text{sub}_{\text{mound}} + b_8.\text{sub}_{\text{stump}} .\text{height}$$

Species	Parameter	Estimate	SE
N. fusca	β_1	1.580	0.407
N. fusca	β_2	3.533	0.587
N. fusca	b_1	5.838	0.811
N. fusca	b_2	–3.827	1.306
N. fusca	β_3	1.027	0.298
N. fusca	b_3	–0.208	0.380
N. fusca	b_4	–0.674	0.377
N. fusca	b_5	–1.900	0.477
N. fusca	β_4	2.027	0.532
N. fusca	b_6	–1.349	0.512
N. fusca	b_7	1.196	0.864
N. fusca	b_8	0.977	0.864
N. menziesii	β_1	0.028	1.673
N. menziesii	β_2	7.107	3.805
N. menziesii	b_1	3.232	1.413
N. menziesii	β_3	0.025	0.404
N. menziesii	β_4	1.018	0.633

Chapter 3 Tree growth in mixed old-growth *Nothofagus* forest in relation to size, competition and disturbance

3.1 Introduction

Tree growth is a key measure of performance, which can also determine rates of reproduction and mortality (Kaitaniemi et al., 1999; Wyckoff and Clark, 2002). As a consequence, patterns of tree growth within and among species play a critical role in determining compositional turnover in the course of forest succession (Pacala et al., 1996; Purves and Pacala, 2008). Understanding growth patterns is necessary to develop predictive models of forest stand dynamics, carbon storage and sequestration, sustainable forest management practices and to forecast timber yield (Pacala et al., 1996; James and Norton, 2002; Purves and Pacala, 2008; Kunstler et al., 2009).

Tree growth is chiefly determined by resource availability and characteristics of individual trees (Oliver and Larson, 1990). At large spatial scales, climate can govern resource availability and tree growth patterns (Canham et al., 2006; Sánchez-Gómez et al., 2008; Gómez-Aparicio et al., 2011; Easdale et al., 2012), but at a local scale, competition with neighbouring trees is the key determinant of growth rate (Canham et al., 2004; Coates et al., 2009). Above-ground size-asymmetric competition for light more adversely affects smaller trees, as they are on average more shaded by larger neighbours (Weiner, 1990). Between species, however, growth varies widely in response to neighbourhood competition. Among species differing in shade-tolerance, a

trade-off between growth in high light (low neighbourhood competition) and survival in low light (high neighbourhood competition) has been frequently documented, especially for relatively small trees (Kobe et al., 1995; Kobe and Coates, 1997; Kneeshaw et al., 2006). Because growth rates of long-lived organisms such as trees can vary considerably across life stages or size classes, performance trade-offs amongst species are also likely to occur with ontogeny (Lusk, 2004; Baraloto et al., 2005; Muller-Landau et al., 2006). The overall consequence of different growth patterns are 'rank-reversals' in performance between species, across resource gradients or life stages, which allow each species in a community to outperform other species in certain situations and may therefore promote coexistence (Nakashizuka, 2001).

In mixed-species and mixed-aged forest, a wide range of tree sizes are present and stands are typically structurally complex (Puettmann et al., 2008). This renders documenting the role of tree size effects on tree growth especially challenging. On average small trees are more shaded by larger neighbours, so it can be difficult to distinguish competitive effects on growth from the inherent ontogenetic variation in growth that may occur across tree sizes (Metcalf et al., 2009; Rüger et al., 2011). Understanding the effects of neighbourhood competition on tree growth can also be difficult when frequent disturbances modify stand structure and species composition. These dynamic stand conditions can lead to inter-annual variation in tree growth rates (e.g., Hartmann and Messier, 2011). Following nearby disturbance, residual (surviving) trees may display increased growth due to release from neighbourhood competition (Wiser et al., 2005; Jones et al., 2009; Noguchi and Yoshida, 2009; Powers et al., 2009). Alternatively, residual trees could have slower growth due to damage sustained in the

disturbance event or related pathogen attack (Jones and Thomas, 2004; Wiser et al., 2005). If the nature of responses to nearby disturbance and gap creation vary among species, then disturbance has the potential to influence the performance ranks of co-occurring species.

A challenge that arises in the analysis of tree growth in mixed-species and mixed-aged forests concerns determining suitable competition indices for use in individual-tree growth models. Individual tree growth rate is typically regressed against characteristics of the individual trees (e.g., diameter, height or crown size) and a competition index to reflect localised stand conditions (Biging and Dobbertin, 1995). Simple competition indices, including measures such as stand basal area or stem density have proven suitable correlates for tree growth in relatively uniform or even-aged stands. More complex, spatially-explicit indices include detailed information on the sizes, abundance and spacing of trees and competition is given as a function of the distance between target and neighbouring trees and their relative sizes (Stadt et al., 2007). By also including data on neighbour identity, spatially explicit competition indices can also be used to examine whether species differ in their competitive effects on a target tree (e.g., Canham et al., 2004). Although they require more detailed data, spatially explicit indices are often most suitable for analysis of structurally complex forests (Canham et al., 2004; Stadt et al., 2007).

To identify performance trade-offs between co-occurring *Nothofagus fusca* and *Nothofagus menziesii*, this study examines how growth varies between species, across size classes, along gradients in local neighbourhood competition and with local

disturbance. A key goal is to determine whether trends in growth observed previously in managed and extensively disturbed mixed-*Nothofagus* forest also occur in unmanaged old-growth forest subject to frequent small-scale disturbances. Competitive effects of neighbours are likely to be most important for small *N. fusca* which is considered more shade intolerant than *N. menziesii* (Wardle, 1984). Previous studies suggest that *Nothofagus* trees quickly respond to increased resources following adjacent canopy gap creation or thinning (Hosking and Kershaw, 1985; Vittoz et al., 2001; Wiser et al., 2005; Easdale et al., 2010). In this study the effect of neighbourhood disturbance is also incorporated into individual-level tree growth models. Based upon patterns observed in even-aged and managed *Nothofagus* forest, *N. menziesii* growth is expected to be most responsive to disturbance following the death of neighbouring trees (Wiser et al., 2005; Easdale et al., 2009; Easdale et al., 2010). Finally, mapped plot data allow us to compare support for neighbourhood competition indices that vary in complexity. To explore whether *N. fusca* and *N. menziesii* are functionally equivalent in their competitive effects on neighbours, neighbourhood competition indices are used that allow for species-specific competitive effects (e.g., Canham et al., 2006).

3.2 Methods

3.2.1 Species, study area and data collection

The study was conducted in low elevation old-growth broadleaved-evergreen (angiosperm) forest in the Maruia Valley, South Island, New Zealand (42°13' S, 172°16' E). Three stands (Pell Stream, Rough Creek, Station Creek) were sampled, all located on alluvial terraces and dominated both in the canopy and in smaller size classes by two species of southern beech (Nothofagaceae): *Nothofagus fusca* (Hook. f.) Oerst. and *N. menziesii* (Hook. f.) Oerst. Together these species co-dominate extensive areas of New Zealand forests and are two of the most dominant indigenous species in terms of basal are and stem density (Peltzer and Payton, 2006; Wiser et al., 2011). *N. fusca* is generally considered less shade tolerant than *N. menziesii*, grows larger (up to 200 cm diameter, 30 m tall v. 150 cm diameter, 25 m tall for *N. menziesii*) and has shorter-lived leaves (1 y v. 3.5 y; Wardle, 1984).

Elevation across the three study sites ranges from 450 to 600 m a.s.l. Mean annual precipitation at nearby Springs Junction (425 m elevation, approximately equidistant to the three study plots) is 2280 mm, with >130 mm recorded every month (National Institute of Water and Atmospheric Research, unpublished data). Mean annual temperature is 9.8ºC, with a monthly minimum of 3.8ºC (July) and monthly maximum of 15.2ºC (January). The valley-floor soils in the study area developed on Pleistocene glacial outwash deposits and contain granite, greywacke and schist (Bowen, 1964); and are acidic (mineral soil pH 4.0) with relatively high levels of available P (Wiser et al., 2005).

In 1986, permanent plots were established in each stand (named "Station Creek", "Rough Creek" and "Pell Stream" plots), each 0.8–1.0 hectares in size. Plots were subdivided into contiguous subplots of 5×5 m, within which all tree stems with a diameter at breast height (DBH, 1.35 m along stem) ≥ 50 mm were labelled using uniquely numbered aluminium tags and their diameter measured using a diameter tape. All three plots were fully re-measured in the austral summers of 2001 and 2009, when all tree stems were re-measured, survival of trees recorded and new recruits (≥ 50 mm DBH) tagged. On the Station Creek plot, tree locations were mapped during plot establishment in 1986, with the *x* and *y* coordinates (to within 0.5 m) of each tree recorded within each 5×5 m subplot. At Pell Stream and Rough Creek trees were mapped in 2009–2010, taking care to locate and map dead trees wherever possible. A small number of dead trees (n=72), typically with a diameter < 10 cm, were not re-located on these plots and for analyses were assigned coordinates corresponding to the middle of the 5×5 m subplot where they were originally recorded.

At the study plots *N. fusca* is most dominant in terms of total basal area (58.0 $m^2\ ha^{-1}$ cf. 14.4 $m^2\ ha^{-1}$ for *N. menziesii* at the beginning of the study in 1986), but *N. menziesii* is dominant in terms of stem density (529 stems ha^{-1} cf. 360 stems ha^{-1} for *N. fusca* in 1986). Through the study period total tree density declined from 915 stems ha^{-1} in 1986, to 829 stems ha^{-1} in 2009. Overall basal area declined from 72.7 $m^2\ ha^{-1}$ in 1986, to 70.3 $m^2\ ha^{-1}$ in 2009. Both species display 'reverse-J' size class frequency distributions, consistent across all three study plots and similar to those reported for a nationally representative sample of mixed *Nothofagus* forest (Wiser et al., 2011).

3.2.2 Data analysis

Observed annual diameter growth (G, mm y^{-1}) of each target tree was calculated based on diameter measurements in 2001 and 2009. For each species, I follow an established approach to model G as a function of target tree size (diameter at breast height, DBH_i; cm), and characteristics of its neighbourhood (Canham et al., 2004; Coates et al., 2009). The full model takes the form:

$$G = P \times Size\ effect \times Neighbourhood\ effect \times Disturbance\ effect$$

(equation 1)

For each species, reduced models (i.e. excluding size, neighbourhood or disturbance effects) were used to assess the relative importance of each model component (see Table 3.1). Full results are reported for the most parsimonious model for each species. P is an estimated parameter for each species interpreted as the theoretical potential growth rate (mm y^{-1}; consistent with the data) of a tree in the least crowded neighbourhood and at the tree size at which maximum growth occurs. The size and neighbourhood effects are scalars between 0–1 that act to reduce the theoretical potential growth rate (Canham et al., 2004; Coates et al., 2009). Because target trees might exhibit compensatory growth following any recent tree deaths in their neighbourhood, the disturbance effect is a scalar ≥ 1 that can increase growth of target trees in disturbed parts of the stand.

The size effect was modelled using a log-normal function: this function allows the shape of the size effect to be either monotonically increasing or decreasing, or humped with a peak at intermediate diameters (Canham et al., 2004; Coates et al., 2009).

$$Size\ effect = e^{-1/2\ \frac{\ln(DBH_i\ \delta)}{\sigma}^{\ 2}} \quad \text{(equation 2)}$$

Parameter δ is the tree diameter, estimated from the data, at which maximum growth is expected to occur, while σ determines the rate at which the function achieves that maximum value (Canham et al., 2004; Canham et al., 2006; Coates et al., 2009). The neighbourhood effect was given by:

$$Neighbourhood\ effect = e^{-C \times NCI^{D} \times DBH_i^{\gamma}} \quad \text{(equation 3)}$$

Equation 3 assumes that growth declines as a function of a neighbourhood competition index (*NCI*, of which several formulations are tested; see below), where parameters *C* and *D*, estimated by the analysis, determine the steepness of the decline in growth with increasing *NCI*. If *D*=1, growth declines as a simple negative exponential function of the *NCI* (Canham et al., 2006; Coates et al., 2009). If *D*>1 the function is sigmoidal and fits an initially slow rate of decline in growth with increasing *NCI*, preceding a steeper rate of decline (Canham et al., 2006; Coates et al., 2009). Fitted values of *C* and *D* cannot be compared between species, because they depend on the parameters of the *NCI* (see below). Equation 3 also allows me to examine whether, for any given degree of neighbourhood competition, the target tree growth response varies with target tree size (Canham et al., 2006; Coates et al., 2009): DBH_i in equation 3 is the

diameter of the target tree, and parameter γ, estimated by the analyses, determines whether either small ($\gamma < 0$) or large ($\gamma > 0$) trees are more sensitive to neighbourhood competition (Canham et al., 2006; Coates et al., 2009). Note that in this study the effects on target tree growth of shading by neighbouring trees was not distinguished from the effects of crowding by neighbouring trees (cf. Canham et al., 2004; Coates et al., 2009). Therefore in the present study, the neighbourhood effect cannot explicitly determine the relative importance of above ground competition for light, versus below ground competition for other resources.

Neighbourhood competition indices

Several alternate formulations of the neighbourhood competition index (*NCI*) were fitted, including two spatially explicit indices and one non-spatial index. I determined which of these received most support before fitting more complex models.

First, the effect of neighbouring trees on target tree growth is assumed to vary with the relative sizes of the target tree, the neighbouring trees (within a fixed circular area), and the distances between them. For *j*=1,…*n* neighbours within a fixed radii of target tree *i*, a neighbourhood competition index can be formulated as:

$$NCI_{standard} = \sum_{j=1}^{n} \frac{DBH_j{}^{\alpha}}{distance_{ij}{}^{\beta}} \qquad \text{(equation 4)}$$

The radius was fixed at 15 m (see Appendix 3.1). Parameters α and β are estimated by the analyses and determine the shape of the effects of neighbour tree size (controlled by α), and distance (controlled by β) on tree growth (Canham et al., 2004).

Second, I tested an index in which neighbours only had a competitive effect if they were larger than the target tree (i.e. only larger trees were included as neighbours; (Canham et al., 2004). This index accounts for the diameter difference between target and neighbouring trees, because large size inequalities would likely be more influential on target tree growth than small size inequalities (Canham et al., 2004):

$$NCI_{asymmetric} = \sum_{j=1}^{n} \frac{DBH_j - DBH_i}{distance_{ij}}^{\alpha\ \beta} \qquad \text{(equation 5)}$$

Finally, the simplest neighbourhood competition index I tried is simply the sum of the basal areas of all neighbours growing within a circular neighbourhood of each target tree. The neighbourhood radius was fixed at 15 m. This simple index assumes that the competitive effect of a neighbour is proportional to its basal area, regardless of its distance from the target tree.

$$NCI_{simple} = \sum_{j=1}^{n} \frac{\pi \times DBH_j^{\,2}}{4} \qquad \text{(equation 6)}$$

Our initial models (Appendix 3.3) indicated that only $NCI_{standard}$ performed well, therefore this index was used in subsequent analyses described below.

Species-specific competitive effects

Established methods were used to adjust $NCI_{standard}$ to account for potential species-specific competitive effects on growth. For i=1,…s species and j=1,…n neighbours of species (or groups of species), s, the species-specific competition index was formulated as:

$$NCI_{standard,species\ specific} = \sum_{i=1}^{s} \sum_{j=1}^{n} \lambda_i \frac{DBH_{ij}^{\ \alpha}}{distance_{ij}^{\ \beta}} \qquad \text{(equation 7)}$$

λ is a species-specific competition coefficient ranging from 0 to 1, allowing for each species (or group of species) of neighbour to differ in their competitive effects (Canham et al., 2004). Because the majority (96.5%) of trees across the study sites were either *N. fusca* or *N. menziesii*, for each target species (*N. fusca* or *N. menziesii*) neighbours were distinguished into two groups: 'conspecific' or 'heterospecific'. Other species (3.5% of total stems) included relatively small sub-canopy species of which >95% of stems present were <20 cm diameter.

Disturbance effect

Recent deaths of trees and subsequent creation of canopy space is likely to release any residual (surviving) neighbouring trees from competition and lead to faster tree growth (Wright et al., 2000). Because of this, in relatively disturbed parts of these old-growth stands, neighbourhood competition indices may poorly explain tree growth rate.

Some analyses of tree growth include only those target trees that grow in relatively intact or un-harvested neighbourhoods (e.g., Canham et al., 2004). In the present study trees in the most disturbed neighbourhoods could also have been excluded, which would result in an improved fit over any model presented here, however exploratory analyses indicated that trees recently partially released from neighbourhood competition grew faster on average than the general population. I did not want to exclude those target trees growing in the more dynamic parts of the stands from the analysis, especially since a primary application of the growth models will be in a simulation model of forest stand dynamics. I identified for each target tree all neighbouring trees that had died in the preceding 1986–2001 interval (based upon annual assessments during this period), then calculated a size and distance dependent disturbance index (*DI*) to account for the effect of previous disturbance (1986–2001) on target tree growth (2001–2009).

$$DI = \sum_{j=1}^{n} \frac{DBH_j{}^{e}}{distance_{ij}{}^{f}} \qquad \text{(equation 8)}$$

Parameters *e* and *f*, estimated by the analyses, determine the effect of neighbouring dead trees size (controlled by *e*) and distance (controlled by *f*), to target tree growth. Only dead neighbouring trees were included in the calculation of *DI*. The disturbance effect was constrained to be ≥1 and was given by:

$$Disturbance\ effect = e^{-E \times DI} - 1 \qquad \text{(equation 9)}$$

Site effects

Stand conditions varied across the three study sites and this pattern is largely attributed to larger patches of relatively dense regenerating *N. menziesii* at Pell Stream than at the other two plots. To determine whether unmeasured site differences lead to systematic differences in growth or neighbourhood effects between the three study plots, I plotted observed vs. fitted growth separately for each of the three study plots, using the best supported model for each species. This procedure did not indicate any major divergence in model fit across plots (see Appendix 3.2), though for *N. menziesii* I noted that a greater proportion of stems had relatively low predicted and observed growth at the Pell stream study site. On the basis of these results I did not include a separate term to account for unmeasured plot effects. For each species I also separately graphed the distribution of model residuals for each of the three study plots. These histograms showed similar distributions across study plots, indicating that the models performed similarly across study plots.

Likelihood estimation and model comparison

To assess the importance of the size, neighbourhood competition and disturbance effects described above, for each species I compared support for a series of models against including a null model (i.e. a model fitting the mean overall growth rate). A total of six models were defined for each species (Table 3.1). The simplest of these models

had a total of two estimated parameters, while the most complex models contained 12 estimated parameters (Table 3.1).

I determined the maximum likelihood parameter estimates of each candidate model equation using simulated annealing, a global optimisation procedure (Goffe et al., 1994). All analyses were done using the R program for statistical computing (v 2.15.1), using the 'likelihood' package (Murphy, 2012), running each model for 150 000 iterations. While errors were normally distributed, heteroscedasticity (i.e. variance increasing with the mean predicted growth rate) was observed for both *N. fusca* and *N. menziesii*. Heteroscedasticity was incorporated by modelling the error term as:

$$\varepsilon_i = X_i^{\sigma} \qquad \text{(equation 10)}$$

X_i is predicted growth for the ith tree, and σ is a maximum likelihood estimate. Models that accounted for heteroscedasticity increased the likelihood so this approach was taken in all models.

Support for each model was examined relative to others in the candidate set, using the small sample version of Akaike's Information Criterion (AIC) and the associated 'Akaike weights' (w_i). AIC works by balancing goodness of fit versus the number of parameters included in a model, where models with the smallest AIC values are those most strongly supported by the data (Burnham and Anderson, 2002). Parsimonious models are favoured over more complex models (i.e. those with more estimated parameters) when $\Delta\text{AIC} \leq 2$. Each Akaike weight, w_i, describes the probability, given the data, of each model being the best in the candidate model set. The slope of observed

vs. predicted growth (with a zero intercept) was used as an indication of model bias (with an unbiased model having slope of 1), and R^2 was used as a measure of goodness-of-fit.

Asymptotic two-unit support intervals were calculated for each of the maximum likelihood parameter estimates as these can also be used to assess support for each of the parameters included in the candidate models (Edwards, 1992). These support intervals indicate the range in each parameter value that would result in an AIC difference of less than two units, and are roughly equivalent to 95% support intervals defined using likelihood ratio tests (Hilborn and Mangel, 1997). For each species, maximum likelihood parameter estimates from the best supported model were used to graph patterns of size dependent growth across the range of tree sizes in the original data. Expected size-dependent growth at the lowest and highest values of *NCI* and *DI* were also graphed.

3.3 Results

3.3.1 Model comparison and fit

For both *N. fusca* and *N. menziesii*, variation in tree growth rate was not well explained by $NCI_{asymmetric}$ (equation 5) or NCI_{simple} (equation 6), especially compared with $NCI_{standard}$, which by comparison performed well for both species (Appendix 3.3). A lack of strong support for NCI_{simple} was interesting since similar indices are commonly used in tree growth studies, especially when spatially explicit neighbourhood

information is unavailable. The lack of support for these indices was not unduly affected by my choice of neighbourhood radius (i.e. 15 m), because additional models using a variety of neighbourhood sizes made no improvement in likelihood (see Table 3.3, Appendix 3.1). All subsequent models with neighbourhood effects were fitted using $NCI_{standard}$.

For *N. fusca*, the AIC and w_i values for the candidate models indicated considerable model selection uncertainty (Table 3.1), with three models having $\Delta AIC<2$ and $w_i>0.1$. The most parsimonious of these three models included only the neighbourhood effect (no size effect); this model is preferable to more complex models as it contains fewer estimated parameters but with little difference in likelihood (i.e. AIC=976.0 cf. 975.4 for the statistically best-supported model; Table 3.1). This model also had equivalent explanatory power ($R^2=0.33$) compared with the more complex models. For *N. menziesii*, the most supported model included size, neighbourhood and disturbance effects and there was no model selection uncertainty (Table 3.1). Of the models tested for *N. menziesii* this model explained the most variation in growth, as measured by R^2 (i.e. $R^2=0.30$, considerably higher than all other models for *N. menziesii*). For both species the selected models produced unbiased estimates of growth, with slope ≈ 1 (Figure 3.1).

For both species, models that explicitly took into account the identities of the neighbouring trees were less supported than simpler models (e.g., a more parsimonious model with $\Delta AIC<2$ is preferred for *N. fusca*, and $\Delta AIC=140.9$ for *N. menziesii*; Table 3.1).

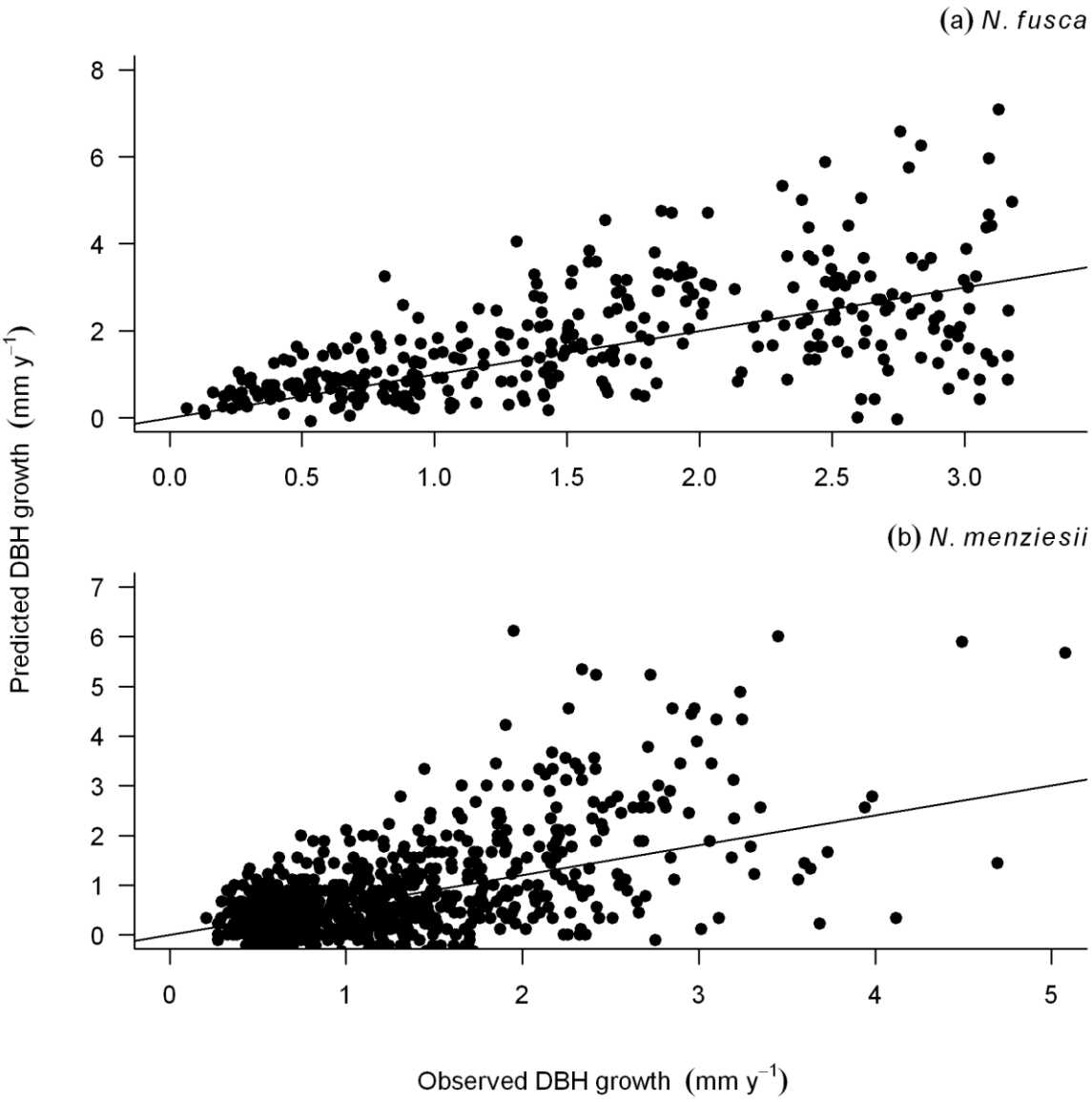

Figure 3.1. Goodness of fit for individual-level growth models for **(a)** *N. fusca* and **(b)** *N. menziesii*, over the 2001–2009 period. Lines show a 1:1 relationship between observed and predicted radial DBH growth (mm y^{-1}).

Table 3.1. Akaike's Information Criterion (AIC) statistics for the candidate set of individual-level models of tree growth (mm y^{-1}) over the 2001–2009 period, for *N. fusca* (n=346) and *N. menziesii* (n=782). Neighbourhood effects were fit using $NCI_{standard}$ (or $NCI_{standard,\ species\ specific}$). K is the total number of estimated parameters in each model (including one parameter for the variance term). ΔAIC is the difference in AIC between each model and the model with the lowest AIC in the candidate set. Parsimonious models are favoured over more complex models (i.e. those with more estimated parameters) when $\Delta AIC \leq 2$. Model weights (w_i) indicate the probability of each model being the best in the candidate set and models with $w_i > 0.1$ are highlighted in bold. For each species * indicates the model used for graphing effects of explanatory variables.

Species	Model	K	AIC	ΔAIC	w_i
N. fusca	Null	2	1228.3	252.8	<0.001
N. fusca	Size effect	4	1009.3	33.9	<0.001
N. fusca	*Neighbourhood effect	7	976.0	0.6	0.313
N. fusca	Size + neighbourhood effect	9	976.7	1.3	0.222
N. fusca	Size + species-specific neighbourhood effects	12	975.4	0.0	0.420
N. fusca	Size +neighbourhood + disturbance effects	12	979.9	4.4	0.046
N. menziesii	Null	2	2358.0	735.9	<0.001
N. menziesii	Size effect	4	2147.3	525.1	<0.001
N. menziesii	Neighbourhood effect	7	1823.3	201.2	<0.001
N. menziesii	Size + neighbourhood effect	9	1756.6	134.5	<0.001
N. menziesii	Size + species-specific neighbourhood effects	12	1763.0	140.9	<0.001
N. menziesii	*Size + neighbourhood + disturbance effects	12	1622.1	0.0	1.000

3.3.2 Variation in growth with size

Mean diameter growth of *N. fusca* was considerably faster than that of *N. menziesii* (mean ± SEM of 1.82 ± 0.076 mm y^{-1} vs. 0.852 ± 0.039 mm y^{-1} respectively). For both species growth increased monotonically with DBH (Figure 3.2). For *N. fusca* inherent growth variation across tree sizes was not a major driver of the strong size-related growth pattern, because the model including size and neighbourhood effects was not strongly supported compared with the model including only neighbourhood effects (Table 3.1). By contrast, for *N. menziesii*, there was a strong relationship between size and growth, with a model including size and neighbourhood effects more supported (lower ΔAIC value; Table 3.1) than models including size or neighbourhood effects alone. Maximum *N. menziesii* growth occurred for the largest trees (e.g. at 79 cm DBH; parameter δ in the best supported model; see Figure 3.2, and Appendix 3.4 for maximum likelihood parameter estimates).

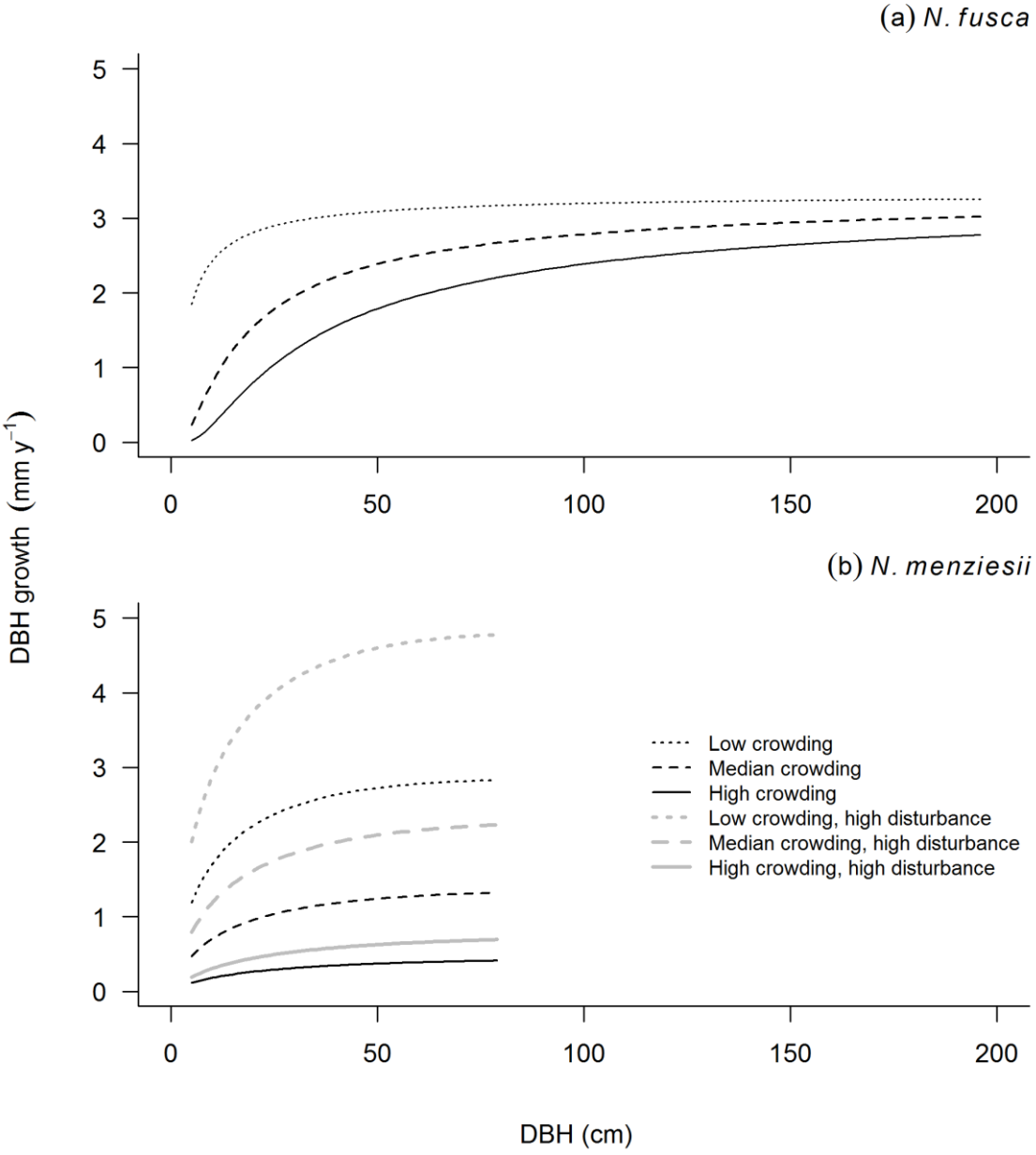
(a) N. fusca
(b) N. menziesii
DBH growth (mm y^{-1})
DBH (cm)
0
1
2
3
4
5
0
50
100
150
200
Low crowding
Median crowding
High crowding
Low crowding, high disturbance
Median crowding, high disturbance
High crowding, high disturbance

Figure 3.2 (previous page). Size-dependent growth (G, mm y^{-1}) versus initial tree diameter (DBH, cm) for **(a)** *N. fusca* and **(b)** *N. menziesii*, predicted using individual-level regressions fit to data over the 2001–2009 period. For each tree, *NCI* was calculated using the parameter estimates for the most parsimonious models (i.e. the 'Neighbourhood effect' model for *N. fusca* and the 'Size + neighbourhood + disturbance effects' model for *N. menziesii*; see Table 3.1). Solid, dashed and dotted lines show predicted growth at low (5% quantile of observed *NCI*), median (50% quantile of observed *NCI*) and high (95% quantile of observed *NCI*) initial neighbourhood crowding respectively (for *N. menziesii*, at median neighbourhood disturbance). For *N. menziesii*, additional thick grey solid, dashed and dotted lines show predicted growth in parts of the stand with a high previous disturbance index (95% quantile of observed *DI*). For each species growth patterns are only graphed across the range of tree diameters in the sample (5–196 cm DBH for *N. fusca* and 5–79 cm DBH for *N. menziesii*).

3.3.3 Effects of neighbourhood competition on tree growth

For both species growth declined as a negative exponential function of the $NCI_{standard}$ competition index. The maximum likelihood estimation for parameter α, which controls the contribution of neighbour size to the overall competitive effect of a neighbour was 0.868 for *N. fusca* and 0.833 for *N. menziesii*. Values for parameter α close to 1 such as these indicate that the competitive effect of each neighbouring tree is roughly proportional to its diameter. Parameter β controls the magnitude of decline in the competitive effects of neighbours with increasing distance from the target tree. For both *N. fusca* and *N. menziesii* neighbourhood effects on tree growth declined dramatically over the 0–15 m distance, but at slower rate for *N. fusca* (β=0.809) than for *N. menziesii* (β=1.079; Figure 3.3).

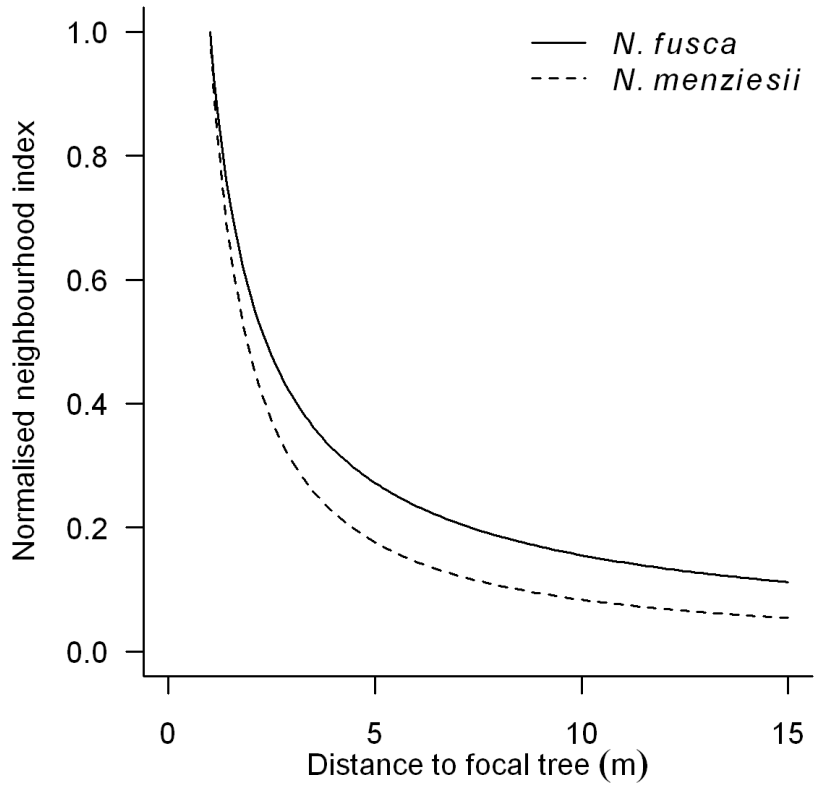

Figure 3.3. Normalised neighbourhood competition index as a function of neighbour displacement (m) from a target tree, for *N. fusca* (solid line) and *N. menziesii* (dashed line), estimated using the maximum likelihood estimates for parameter β in the most parsimonious growth models (β=0.809 for *N. fusca* and 1.079 for *N. menziesii*).

3.3.4 Variation in sensitivity to neighbourhood competition with size

For both species, parameter γ was negative indicating that smaller rather than larger trees were more sensitive to competition. However γ varied between species and was most negative for *N. fusca* (–0.902) compared with *N. menziesii* (–0.072). This result is indicative of much stronger sensitivity to competition for small rather than large *N. fusca*. Indeed for the smallest *N. fusca* (~5 cm DBH), modelled growth of trees in the least crowded neighbourhoods was more than 70-fold that of trees in the most crowded neighbourhoods, decreasing to a 10-fold difference for trees ~10 cm DBH, and a less than two-fold difference for trees greater than ~36 cm DBH (Figure 3.2). For relatively large (>100 cm DBH) *N. fusca* there was little difference in the growth rates of trees in the least vs. most crowded neighbourhoods (Figure 3.2). By contrast, for *N. menziesii* a γ value of –0.072 is not indicative of strong variation in sensitivity to competition across tree sizes. For *N. menziesii*, for example estimated differences in growth between trees in the least vs. most crowded neighbourhoods ranged from more than ten-fold for relatively small (~5 cm DBH) trees, to approximately seven-fold for relatively large (~75 cm DBH) trees (Figure 3.2).

3.3.5 Neighbourhood disturbance effects

For *N. menziesii*, the importance of compensatory growth following neighbourhood disturbance was revealed by much stronger support for a model that included the disturbance effect, compared with all other models (e.g., w_i=1.000 and ΔAIC of all other models ≥134.5; Table 3.1). *N. menziesii* trees growing in parts of the

stands with high previous disturbance (e.g. 0.95 quantile of *DI*) grew faster on average (mean ± SEM of 2.84 ± 0.027 mm y^{-1}) than those growing in relatively stable parts of the stands (e.g., 0.05 quantile of *DI*; mean ± SEM of 0.80 ± 0.19 mm y^{-1}). For *N. fusca* by contrast there was no evidence of faster growth in recently disturbed neighbourhoods, as the model containing the disturbance effect was less supported than more parsimonious models (ΔAIC=3.4; Table 3.1).

3.4 Discussion

3.4.1 Competition and disturbance effects on growth

Previous studies have shown that the effect of neighbour displacement on individual growth varies amongst relatively shade-intolerant and shade-tolerant species, (e.g., Simard and Sachs, 2004; Boivin et al., 2010). This may be a generally occurring trend. For both species in this study the distance-dependent component of the $NCI_{standard}$ competition index showed that the effect of a neighbour on target tree growth declined rapidly with increasing displacement, but at a slower rate for the shade-intolerant *N. fusca* target trees than the shade-tolerant *N. menziesii* target trees, as shown by the maximum likelihood estimates for parameter β in this study (i.e. *N. fusca* growth is influenced more strongly than *N. menziesii* growth by distant neighbours).

It is noteworthy that for both *N. fusca* and *N. menziesii*, the only neighbourhood competition index that explained individual tree growth was a size and distance dependent index ($NCI_{standard}$); simpler indices were uninformative. Spatially-explicit

competition indices may generally perform better than simpler non-spatial indices when stand structure is heterogeneous and non-uniform such as in old-growth stands (Busing and Mailly, 2004; Hartmann et al., 2009). This may explain why previous studies of *Nothofagus* growth, without using spatial explicit competition indices, have not always found significant effects of stand basal area on growth (e.g., Hurst et al., 2007).

The effect of neighbour tree size on individual tree growth, determined by parameter α, was roughly equivalent for both target species (α=0.83 for *N. fusca* vs. 0.87 for *N. menziesii*) and indicated that for each target species the perceived competitive effect of each neighbour is roughly proportional to the neighbour's diameter. Crown radius of both species is approximately a linear function of diameter (unpublished data); estimated α values close to one therefore indicate that the effect of neighbours on target tree growth of both species is also approximately linearly related to their crown radii. Crown radius reflects a trees canopy position and ability to outcompete neighbouring trees for light. My results therefore reveal the size-structured nature of competition between neighbours in these stands, such that large neighbours have greater competitive effects on small trees than vice versa.

Our expectation that growth of small trees of the shade-intolerant *N. fusca*, would be more strongly influenced by neighbourhood effects than growth of large trees, as indicated by the parameter γ, was met. In contrast, the growth of small shade-tolerant *N. menziesii* trees was no more strongly influenced by neighbourhood effects than was the growth of large trees. This result is somewhat inconsistent with observations of *N. menziesii* from monospecific stands where growth of small *N. menziesii* was strongly

influenced by competitive effects of neighbours whereas large *N. menziesii* growth was more strongly influenced by climatic effects (Easdale et al., 2012). In the mixed *Nothofagus* forest studied here the maximum size attained by *N. fusca* far exceeds that of the largest *N. menziesii*, therefore even large *N. menziesii* in the present study tend to be shaded by large neighbours, which may be less likely in monospecific stands. Also, the plot data used by Easdale et al. (2012) allowed only relatively simple neighbourhood competition indices to be used, similar to those found uninformative in the present study. Clearly, the use of size and distance dependent index competition indices will improve our ability to detect competitive effects in forests more generally.

While on average *N. fusca* displayed faster growth than *N. menziesii* across all tree diameters, the intraspecific variation in growth that resulted from the effects of competition and disturbance lead to shifts in the relative performance of each species with ontogeny. At high competition for example, across all diameters, *N. fusca* performed much better than *N. menziesii*, but at low competition the difference was far less marked, especially for relatively large trees. When recent disturbance was considered, the subpopulation of *N. menziesii* that grew in the least crowded and most disturbed stands performed better than *N. fusca*, across all diameters. Therefore the relative performance of these co-occurring species depends on both competition and disturbance.

Several previous studies have examined growth responses of *N. fusca* and *N. menziesii* in forests similar to those studied here following episodes of more severe and extensive disturbance. Hosking and Kershaw (1985) measured growth of both

species in mixed-species stands that suffered severe dieback and compared these to growth rates in undamaged stands. No difference in *N. fusca* growth was found between damaged and undamaged stands, but *N. menziesii* growth following canopy dieback markedly exceeded growth rates prior to canopy dieback. Vittoz et al. (2001) measured growth of both species after a major earthquake and similarly found that growth releases were much more frequent in *N. menziesii* than *N. fusca*. Similarly Wiser et al. (2005) found greater responses following experimental small-coupe harvesting for residual trees of the shade-tolerant *N. menziesii*, than for *N. fusca* (or *N. truncata*). Although the type and magnitude of a disturbance event may determine the extent of compensatory growth responses in surviving neighbouring trees (Vittoz et al., 2001), this study shows that the types of differential responses to disturbance seen previously in *N. fusca* and *N. menziesii* are also apparent in stands subject to relatively small-scale infrequent natural disturbance events.

Rank reversals in growth between species along competition and disturbance gradients would be expected to have profound consequences for community dynamics. Individual tree growth rate is a strong predictor of the likelihood of mortality for both species, but especially for *N. fusca* (Hurst et al., 2012). Furthermore, increased *N. fusca* mortality is likely in disturbed parts of the stand (Hurst et al., 2012). Disturbance in mixed *Nothofagus* forest has previously been considered to favour dominance by *N. fusca* because of faster juvenile diameter and height growth in canopy gaps (Stewart and Rose, 1990; Runkle et al., 1997). The finding that growth of *N. menziesii* canopy trees is faster than that of *N. fusca* in disturbed neighbourhoods, suggests that disturbance is

likely to favour each species at a different life stage. These different patterns of growth and mortality may play an important role in promoting the coexistence of these species.

3.4.2 Species-specific competitive effects

Theories of species coexistence emphasise that intraspecific competition should be stronger than interspecific competition (Amarasekare, 2003); if this were the case then neighbour identity should be an important determinant of individual tree growth rates. Contrary to this expectation there was no strong evidence that neighbourhood effects on target tree growth varied between conspecific vs. heterospecific neighbours (i.e. for both *N. fusca* and *N. menziesii* the model including species-specific competitive effects was less supported than other models). This result is in contrast to several studies elsewhere showing significant differences in competitive effects between species (Canham et al., 2006; Zhao et al., 2006; Coates et al., 2009).

3.4.3 Model performance

The proportion of growth variation that can be explained by any analytical method is dependent on the ecology and life-stages of the species and the explanatory variables included. Tree growth can be influenced by many factors unaccounted for by the present study, such as climate, disease, individual genetic variation and historical factors including performance at early life stages (Landis and Peart, 2005). Nevertheless the

final model fits compare satisfactorily with previous growth studies undertaken for these species (e.g., R^2=0.32 for *N. fusca* and 0.30 for *N. menziesii*). For example, for *N. menziesii*, previous studies report R^2 values of 0.31–0.42 (e.g., in models including climatic variables; Easdale et al., 2012), and 0.29 (Wiser et al., 2005); while for *N. fusca* previous studies report R^2 values of 0.15 (Wiser et al., 2005). Similar modelling approaches used in forests elsewhere have yielded R^2 values of between 0.10–0.82, varying amongst species and life-stages (Canham et al., 2004; Uriarte et al., 2004; Canham et al., 2006; Papaik and Canham, 2006; Boivin et al., 2010).

3.4.4 Implications for forest management and modeling

To determine whether forest management regimes for timber production are appropriate, any long-term compositional or structural changes driven by management activities need to be understood, which can be challenging in mixed-species and mixed-aged forests. The present study suggests that harvesting could substantially alter the relative performance of these species in stands where they co-occur. Amongst species distinct differences were found in growth relationships with size, competition and disturbance. *N. fusca* small tree growth rates are most influenced by competition with neighbours, but fast growth of large *N. menziesii* occurs in proximity to natural canopy disturbance (i.e. the death of neighbouring trees). In managed forest *N. menziesii* growth also increases when in close proximity to gaps created through harvesting (Wiser et al., 2005). Silvicultural treatments (e.g., thinning) to reduce tree density can also increase growth of New Zealand's *Nothofagus* species, but so far such activities have been

confined to relatively young, even-aged stands (e.g., Easdale et al., 2009, 2010). My results suggest that thinning operations may increase growth of *N. menziesii*, across a much wider range of tree sizes than has previously been considered, which could lead to greater yield in managed forests.

How would more frequent disturbances, such as those created by patch cuts and group selection, influence the long-term dynamics of these forests? The community-level consequences of management can be studied using individual-based simulation models. Individual-tree growth models (along with recruitment and mortality models) must capture the key relationships between tree size, neighbourhood competition and disturbance. My results demonstrated that simple non-spatially explicit competition indices were inadequate for describing competitive interactions between neighbouring trees in these mixed forests. This implies that if accurate predictive modelling is required to support forest management decision making, spatially explicit simulation models will be required.

Appendix 3.1 Support for alternate neighbourhood radii

The choice of neighbourhood radii to use in tree growth analyses presents a compromise between the scale of neighbour interactions that can be included, versus any subsequent decrease in sample size (as neighbour information for trees growing near plot edges is incomplete and these trees must be excluded from analyses). In this study the neighbourhood radius was fixed at 15 m and trees growing within 15 m from plot edges were excluded. It is notable that the 15 m radius used in the present study to represent neighbourhood competition effects on growth is much larger than is usually available from permanent plot datasets: plot systems most commonly used throughout New Zealand (see Wiser et al., 2001), typically comprise much smaller plots (e.g., typically 20 ×20 m) than used in the present study. To examine support for neighbourhood competition indices at smaller scales in the study system forests, a sequence of alternate models were fit with neighbourhood competition indices calculated across scales of 5–15 m radii. This was done separately for two competition indices, $NCI_{standard}$ (the best supported index) and NCI_{simple} (a non-spatial index). The lack of support for NCI_{simple} (see method and results) was surprising in this study, so it was prudent to check that this result was not unduly affected by the neighbourhood radii selected to fit the model. By using the same data and model structure for each sequence of models, the results can be directly compared using Akaike's Information Criterion (AIC). Models within two AIC units of one another can generally be considered to have equivalent support (Burnham and Anderson, 2002). Any further reduction in neighbour competitive effect at distances greater than 15 m was not examined. Although competitive interactions could also occur over larger distances, the competitive effect of

neighbours growing 15 m from a target tree is relatively minimal (see results, Figure 3.2).

Alternate neighbourhood radii comparison when using $NCI_{standard}$

When $NCI_{standard}$ was used as the competition index the choice of maximum neighbourhood radii influenced support across models. For *N. fusca*, there was considerable model selection uncertainty and no one model received strong support: neighbourhood radii of 11–15 m were supported, for which together $\sum w_i$=1.0 (Table 3.2). For *N. menziesii* a neighbourhood radii of 14 m was much more supported than any other radii tested (w_i =0.92; Table 3.2). Model goodness-of-fit, across all radii tested varied least for *N. fusca* (R^2 of 0.32–0.36; Table 3.2). For *N. menziesii* R^2 appeared generally higher for models using the larger neighbourhood radii (R^2 ranges between 0.17–0.23, and Table 3.2).

Alternate neighbourhood radii comparison when using NCI_{simple}

When NCI_{simple} was used as the competition index, the choice of maximum neighbourhood radii had no influence on overall model fit. For both species the model selection statistics showed little difference in AIC across neighbourhood radii scales of 5–15 m, regardless of the radius used (Table 3.3). Furthermore, and confirming the previous result (see results), for both species, all models using NCI_{simple} remained unsupported compared to other models tested. Poor support for models that used NCI_{simple} (see main results) was therefore not due to the 15 m radius selected for calculation of the index.

Table 3.2. Akaike's Information Criterion (AIC) statistics for individual-level models of tree growth (mm y^{-1}) over the 2001–2009 period, for *N. fusca* (n=346) and *N. menziesii* (n=782); using the standard distance and size dependent neighbourhood competition index ($NCI_{standard}$), but omitting any size effect (see methods). The total number of estimated parameters in all models is 7; models only differ in the size of the neighbourhood used to calculate $NCI_{standard}$, with neighbourhood radii ranging from 5–15 m. ΔAIC is the difference in AIC between each model and the best supported model in the candidate set, with the best supported model having ΔAIC of zero. Model weights (w_i) indicate the probability of each model being the best in the candidate set. Models with w_i >0.1 are in bold. R^2 and slope statistics are for the observed vs. fitted values.

Species	Radius (m)	AIC	ΔAIC	w_i	Slope	R^2
N. fusca	15	976.0	0.0	0.36	1.07	0.33
N. fusca	14	976.9	0.9	0.23	1.08	0.33
N. fusca	13	977.3	1.3	0.18	1.05	0.34
N. fusca	12	977.6	1.6	0.16	1.08	0.33
N. fusca	11	979.5	3.5	0.06	1.06	0.34
N. fusca	10	983.7	7.7	0.01	1.04	0.34
N. fusca	9	987.8	11.8	0.00	1.05	0.33
N. fusca	8	993.2	17.2	0.00	1.06	0.33
N. fusca	7	1005.0	29.0	0.00	1.08	0.32
N. fusca	6	1005.5	29.5	0.00	1.05	0.32
N. fusca	5	1010.0	34.0	0.00	1.06	0.31
N. menziesii	15	1823.3	12.6	0.00	1.01	0.21
N. menziesii	14	1810.7	0.0	0.92	1.03	0.23
N. menziesii	13	1827.9	17.2	0.00	1.03	0.22
N. menziesii	12	1829.8	19.1	0.00	1.03	0.23
N. menziesii	11	1815.5	4.8	0.08	1.05	0.22
N. menziesii	10	1842.5	31.8	0.00	1.03	0.21
N. menziesii	9	1839.6	28.9	0.00	1.02	0.20
N. menziesii	8	1876.8	66.1	0.00	1.01	0.18
N. menziesii	7	1900.2	89.5	0.00	1.02	0.18
N. menziesii	6	1928.4	117.7	0.00	1.00	0.18
N. menziesii	5	1955.6	144.9	0.00	1.00	0.17

Table 3.3. Akaike's Information Criterion (AIC) statistics for individual-level models of tree growth (mm y^{-1}) over the 2001–2009 period, for *N. fusca* (n=346) and *N. menziesii* (n=782) using a simple neighbourhood competition index (NCI_{simple} and omitting the size effect, see method and results). The total number of estimated parameters in all models is 7; models only differ in the size of the neighbourhood used to calculate NCI_{simple}, with neighbourhood radii ranging from 5–15 m. ΔAIC is the difference in AIC between each model and the best supported model in the candidate set, with the best supported model having ΔAIC of zero. Model weights (w_i) indicate the probability of each model being the best in the candidate set. R^2 and slope statistics are for the observed vs. fitted values.

Species	Radius (m)	AIC	ΔAIC	w_i	Slope	R^2
N. fusca	15	1234.4	0.0	0.1	1.0	0.00
N. fusca	14	1234.4	0.0	0.1	1.0	0.00
N. fusca	13	1234.4	0.0	0.1	1.0	0.00
N. fusca	12	1234.4	0.0	0.1	1.0	0.00
N. fusca	11	1234.4	0.0	0.1	1.0	0.00
N. fusca	10	1234.4	0.0	0.1	1.0	0.00
N. fusca	9	1234.4	0.0	0.1	1.0	0.00
N. fusca	8	1234.4	0.0	0.1	1.0	0.00
N. fusca	7	1234.4	0.0	0.1	1.0	0.00
N. fusca	6	1234.4	0.0	0.1	1.0	0.00
N. fusca	5	1234.4	0.0	0.1	1.0	0.00
N. menziesii	15	2165.6	0.0	0.8	0.9	0.07
N. menziesii	14	2167.8	2.2	0.2	0.9	0.08
N. menziesii	13	2200.0	34.4	0.0	0.9	0.07
N. menziesii	12	2209.2	43.6	0.0	0.9	0.07
N. menziesii	11	2188.3	22.7	0.0	0.9	0.06
N. menziesii	10	2329.0	163.5	0.0	1.0	0.03
N. menziesii	9	2356.5	190.9	0.0	1.1	0.01
N. menziesii	8	2338.1	172.5	0.0	1.0	0.03
N. menziesii	7	2255.6	90.0	0.0	0.9	0.02
N. menziesii	6	2304.6	139.0	0.0	0.9	0.02
N. menziesii	5	2323.9	158.4	0.0	0.9	0.02

Appendix 3.2 Observed vs. fitted values and residuals across plots.

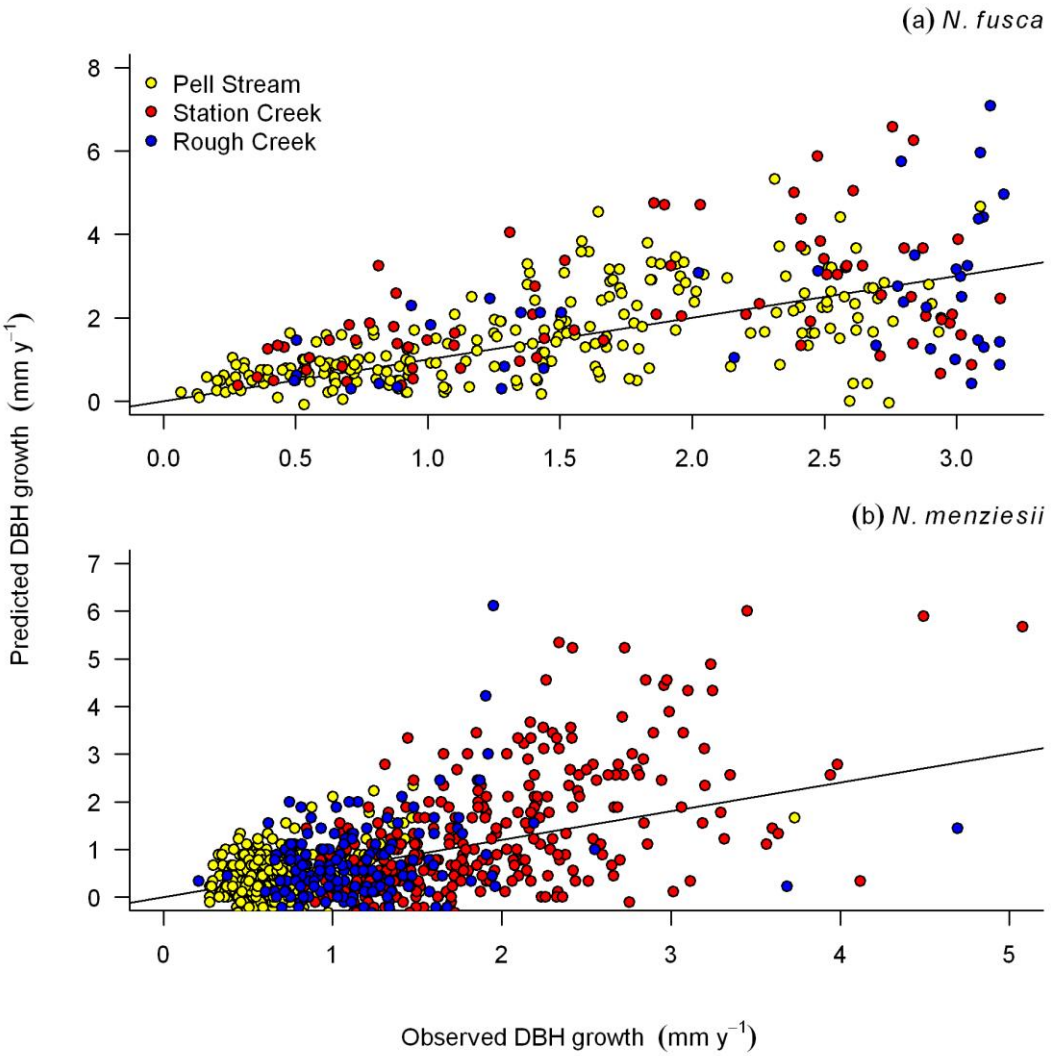

Figure 3.4. Goodness of fit for the best supported candidate growth models (see main text, table 3.1), for **(a)** *N. fusca* and **(b)** *N. menziesii*, over the 2001–2009 period. Lines show a 1:1 relationship between predicted and observed radial growth. Circle colours indicate the three study sites (yellow=Pell Stream, red=Station Creek, blue=Rough Creek). Variation in observed vs. predicted growth amongst sites for *N. menziesii* arises from patches of dense relatively small, slow growing trees at the Pell Stream study site, and more frequent disturbance at the Station creek study site.

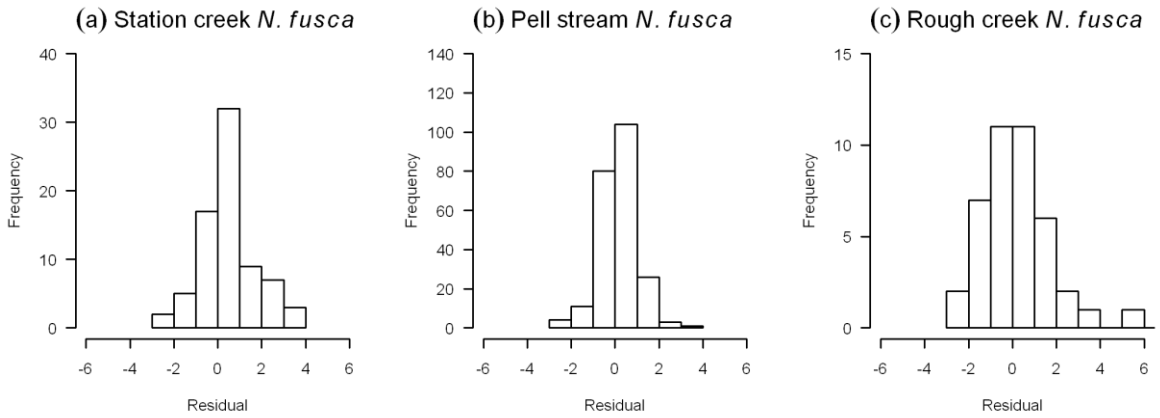

Figure 3.5. Distribution of residuals for *N. fusca*, graphed separately for **(a)** Station creek, **(b)** Pell stream and **(c)** Rough creek.

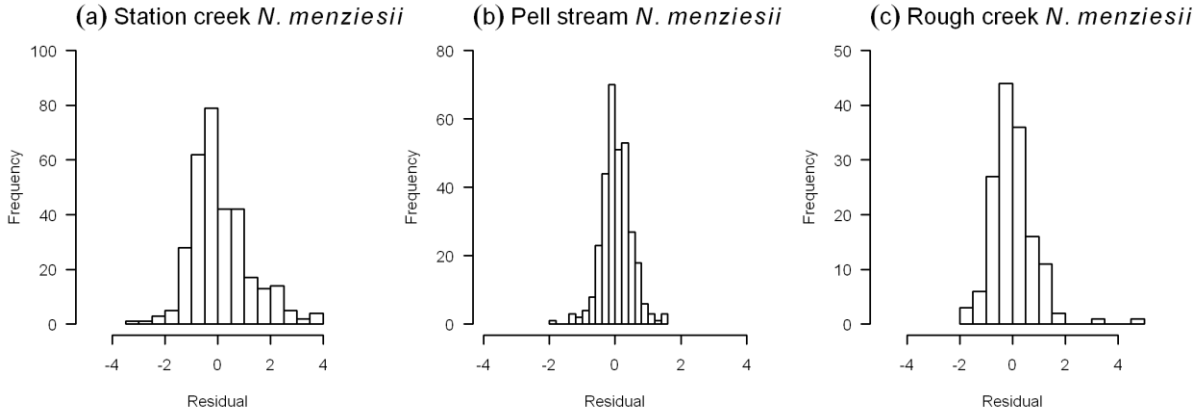

Figure 3.6. Distribution of residuals for *N. menziesii*, graphed separately for **(a)** Station creek, **(b)** Pell stream and **(c)** Rough creek.

Appendix 3.3 Support for alternate NCI indices

Table 3.4. Akaike's Information Criterion (AIC) statistics for individual-level models of tree growth (mm y^{-1}) over the 2001–2009 period, for *N. fusca* (n=346) and *N. menziesii* (n=782), for models using a neighbourhood effect with alternative *NCI* indices: $NCI_{standard}$, $NCI_{asymetric}$, and NCI_{simple}. The null model fits the overall mean growth rate. K is the total number of estimated parameters in each model (including one parameter for the variance term). ΔAIC is the difference in AIC between each model and the model with the lowest AIC in this candidate set. Model weights (w_i) indicate the probability of each model being the best in this candidate set. The best supported models are highlighted in bold.

Species	Model	K	AIC	ΔAIC	w_i
N. fusca	Null	2	1228.3	252.3	<0.001
N. fusca	Neighbourhood effect using $NCI_{standard}$	7	976.0	0.0	1.000
N. fusca	Neighbourhood effect using $NCI_{asymmetric}$	7	1238.6	262.5	<0.001
N. fusca	Neighbourhood effect using NCI_{simple}	5	1234.4	258.4	<0.001
N. menziesii	Null	2	2358.0	534.7	<0.001
N. menziesii	Neighbourhood effect using $NCI_{standard}$	7	1823.3	0.0	1.000
N. menziesii	Neighbourhood effect using $NCI_{asymmetric}$	7	2368.1	544.8	<0.001
N. menziesii	Neighbourhood effect using NCI_{simple}	5	2165.6	341.9	<0.001

Appendix 3.4 Maximum likelihood parameter estimates.

Table 3.5. Maximum likelihood parameter estimates and two-unit asymptotic support intervals (in parentheses) for the most parsimonious model (see Table 1, main text) for *N. fusca* and *N. menziesii* tree growth over the 2001–2009 period. See the main text for a description of each parameter.

Species	Parameter	Estimate	Two-unit support interval
N. fusca	*P*	3.33	3.16–3.63
N. fusca	γ	–0.902	–0.946– –0.865
N. fusca	α	0.868	0.824–0.928
N. fusca	β	0.809	0.777–0.851
N. fusca	*C*	4.01	3.68–4.25
N. fusca	*D*	1.00	1.00–1.05
N. fusca	*σ*	0.606	0.491–0.711
N. menziesii	*P*	1.60	1.54–1.67
N. menziesii	γ	–0.0723	–0.0863– –0.0589
N. menziesii	*δ*	79.0	70.7–79.0
N. menziesii	*σ*	2.25	2.16–2.39
N. menziesii	α	0.833	0.817–0.858
N. menziesii	β	1.08	1.08–1.09
N. menziesii	e	1.11	1.07–1.14
N. menziesii	f	0.937	0.927–0.946
N. menziesii	*C*	0.376	0.364–0.385
N. menziesii	*D*	1.00	1.00–1.01
N. menziesii	*E*	–1.25	–1.31– –1.18
N. menziesii	*σ*	0.820	0.763–0.888

Chapter 4 Determinants of tree mortality in mixed old-growth *Nothofagus* forest[1]

4.1 Introduction

Demographic patterns and processes drive much of the spatial and temporal variation observed in forests. Tree deaths, for example, create canopy gaps and microhabitats for tree recruitment that leave legacies in forest composition and structure (Runkle, 1985; White and Pickett, 1985; Veblen, 1992). In mixed-species forest, different responses among species to such events will ultimately determine the course of forest dynamics. At juvenile life stages (e.g., seedlings, saplings and small trees) for example, interspecific trade-offs in demographic performance (i.e. growth and mortality) are well documented and occur across forest microhabitat and light gradients (Pacala et al., 1994; Lin et al., 2002). Juveniles of shade-tolerant species often have low mortality under low light conditions but only moderate growth responses to canopy openings, whereas juveniles of shade-intolerant species often have high mortality under low light but exhibit strong growth responses to canopy openings (Kobe et al., 1995; Kobe and Coates, 1997; Kneeshaw et al., 2006). These interspecific differences in

[1] This Chapter has been published: Hurst, J.M., Stewart, G.H., Perry, G.L.W., Wiser, S.K., Norton, D.A., 2012. Determinants of tree mortality in mixed old-growth *Nothofagus* forest. Forest Ecology and Management 270, 189–199.

juvenile demographic performance represent an important axis of niche differentiation (e.g., 'the regeneration niche'; Grubb, 1977), which influences the dynamics of mixed-species forests and may promote species' coexistence (Pacala et al., 1996). However, demographic rates also vary intraspecifically, especially, for example, with ontogeny (Boyden et al., 2009). As a consequence, performance differences among species are possible at many life stages. There remains a need to examine performance across a range of tree life-stages to comprehensively explain coexistence (Veblen, 1986; Abe et al., 1998; Lusk and Smith, 1998; Nakashizuka, 2001; Condit et al., 2006).

The mortality probability of an individual tree is commonly examined as a function of readily measured variables such as tree size, recent growth, and the spatial pattern of trees or competitive neighbourhood (Yao et al., 2001; Bigler and Bugmann, 2003; Wunder et al., 2008). More specifically, the importance of density-dependent mortality is often explored by studying changes in the spatial patterning of trees within a stand through time, or amongst stands of different ages (e.g. Gray and He, 2009); or by incorporating variables that describe the competitive neighbourhood into models of individual tree mortality (e.g. Monserud, 1976; Yao et al., 2009). Density dependent competition can often be inferred when the spatial pattern of surviving trees becomes more regular through time (Duncan, 1991; He and Duncan, 2000). For small trees it may be generally the case that competitive interactions drive such patterns of mortality; however, for relatively large trees it is usually difficult to determine a single direct cause of tree mortality (Franklin et al., 1987). Size-asymmetric competition for light is likely to be a relatively unimportant cause of mortality of established large canopy trees (Coomes et al., 2003), particularly in old-growth forest, where mortality results from a

wide range of biotic and abiotic factors including pathogen or insect attack, mechanical failure, and disturbance (Franklin et al., 2002; Busing, 2005). Furthermore, mortality in old-growth forests often operates contagiously, as evidenced by the progressive expansion of canopy gaps (Runkle, 1985, 1998). Spatial patterns of tree mortality, and interactions with previous canopy disturbances, could also be expected to vary interspecifically, for example due to pathogen host-specificity and differing susceptibility of species to wind-throw (Canham et al., 2001; Worrall et al., 2005). Because spatial patterning of mortality events in turn influences microhabitats and light availability, and so has ongoing consequences for forest dynamics, spatial patterns of mortality must be considered in combination with tree size and competition, when examining species-specific patterns.

This study examines tree mortality for two southern beech species, *Nothofagus menziesii* (Hook. f.) Oerst. and *N. fusca* (Hook. f.) Oerst., which co-dominate extensive old-growth mixed-species forests in New Zealand. These are two of the most abundant tree species in New Zealand's remaining indigenous forest (Wardle, 1984; Ogden et al., 1996; Wiser et al., 2011) and such mixed-*Nothofagus* forest comprises > 80% of privately owned indigenous forests managed for timber production (Ministry of Agriculture and Forestry, 2009). There is ongoing debate about the extent to which mortality of New Zealand *Nothofagus* spp. can be predicted, or pre-empted, in managed forests (Mason, 2000), as well as what impact silvicultural harvest will have on remaining canopy trees (Wiser et al., 2005). Large-scale forest dieback events in *Nothofagus* have been documented (Hosking and Kershaw, 1985; Jane and Green, 1986; Ogden et al., 1996), but mortality rates of *N. fusca* and *N. menziesii* trees have

seldom been quantified in the forests where they co-occur. Previous demographic research in mixed-*Nothofagus* forests has focused largely on regeneration patterns and tree growth (e.g., Runkle et al., 1995, 1997; Stewart et al., 1991). Because *N. fusca* is considered relatively shade intolerant, and *N. menziesii* relatively shade tolerant, these species are considered to occupy different regeneration niches (Holloway, 1954; Wardle, 1984; Stewart and Rose, 1990; Ogden et al., 1996; Wiser et al., 2007), although both *N. fusca* and *N. menziesii* require canopy gaps to attain the canopy (Stewart and Rose, 1990; Stewart et al., 1991; Runkle et al., 1995, 1997).

Using data collected over 23 years from tagged *N. menziesii* and *N. fusca* trees on permanently marked plots (Stewart, 1992), we examine how mortality varied between the two species and with tree size. Because asymmetric competition for light is likely to be an important cause of mortality in small trees, a reasonable expectation is that the mortality of small trees will be highest in areas of intense neighbourhood competition; we expect that this will be particularly apparent for shade-intolerant *N. fusca,* in contrast to shade-tolerant *N. menziesii* (Hypothesis 1). Mortality of large individuals is likely to be driven by disturbance rather than competition for light (Franklin et al., 1987; Coomes et al., 2003). If previous disturbance increases subsequent mortality risk then trees growing in disturbed stands will likely have much higher mortality than average (Hypothesis 2), and where disturbance kills multiple trees large dead trees are likely to be spatially aggregated, and segregated from living trees (Hypothesis 3). Finally, native *Platypus* spp. (Platypodidae) beetles attack *Nothofagus* individuals and provide a vector for infection by pathogenic *Sporothrix* fungi, which in turn infect the inner sapwood of trees and lead to their death or stem rot (McCracken et al., 1994). In forests managed for

timber, it has been suggested that new *Platypus* infections of living trees usually occur within 5 m of a previous host tree, large trees are more frequently infected than small trees, and *N. fusca* is more frequently attacked than *N. menziesii* (Litchwark, 1978; McCracken et al., 1994; Wiser et al., 2005). However, little is known about the spatial dynamics of *Platypus* infection in unmanaged forests (McCracken et al., 1994). Based on the dynamics of managed forests, we hypothesize that tree mortality resulting from *Platypus* attack will be spatially clustered, especially for *N. fusca* (Hypothesis 4).

4.2 Materials and methods

4.2.1 Species, study area and data collection

The study was conducted in low elevation old-growth mixed *Nothofagus* forest in the Maruia Valley, South Island, New Zealand (42°13' S, 172°16' E). The study sites (Pell Stream, Rough Creek, and Station Creek) were located on relatively flat and fertile alluvial terraces and were dominated, across all tree size classes, by *N. fusca* and *N. menziesii*. *N. fusca*, considered less shade-tolerant than *N. menziesii*, grows larger (e.g. the largest trees recorded are > 200 cm diameter (*D*), 35 m tall vs. 150 cm diameter, 25 m tall for *N. menziesii*) but is thought to have a shorter maximum longevity (Wardle, 1984). The maximum tree diameter in the present study was 230 cm for *N. fusca* and 80 cm for *N. menziesii*, and size-class structures for both were similar to those reported for a nationally representative sample of mixed *Nothofagus* forest (Wiser et al., 2011).

Elevation across the three study sites ranges from 450 to 600 m a.s.l. Mean annual precipitation at nearby Springs Junction (425 m elevation, approximately equidistant to the three study plots) is 2280 mm, with > 130 mm recorded every month (National Institute of Water and Atmospheric Research, unpublished data). Mean annual temperature is 9.8°C, with a monthly minimum of 3.8°C (July) and monthly maximum of 15.2°C (January). Valley-floor soils developed on Pleistocene glacial outwash deposits contain granite, greywacke, and schist (Bowen, 1964). These soils are acidic (mineral soil pH 4.0) with relatively high levels of available P.

At each of the three sites a permanent plot was established in 1986, each plot being 0.8–1.0 ha in size (100 × 80 m, 150 × 60 m and 100 × 100 m). Plots were subdivided into contiguous subplots of 5 × 5 m, within which all trees ($D \geq 5$ cm) were uniquely tagged, identified and measured. On the Station Creek plot, tree locations were mapped, recording x and y coordinates (to within 0.5 m) within each 5 × 5 m subplot during plot establishment in 1986, whereas at Pell Stream and Rough Creek trees were mapped in 2009–2010, taking care to locate and map dead trees wherever possible. Across these two plots a small number ($n = 72$) of dead trees, typically with $D < 10$ cm, were not re-located, and for analyses were assigned a location at the middle of the 5 × 5 m subplot where they were originally recorded. In 2001 and 2009 the diameter of each tagged tree was remeasured, and recruitment of new individuals ($D \geq 5$ cm) determined. In 2001 and 2009 the new recruits were tagged, measured and their location recorded.

Mortality censuses recorded the fate of each tagged individual during the austral summers of 1987–1998, 2001 and 2009. During each mortality census, stem and crown

debris for trees that had died since the preceding census were examined and the incidence of *Platypus* infection recorded. *Platypus* infection was evidenced by the presence of 'frass' and small borer holes (e.g., 1–2 mm in diameter; McCracken et al., 1994). Dead trees were categorised as either 'standing with intact crown', 'standing with bole broken', 'uprooted' or 'crushed by falling neighbouring trees or branches'.

4.2.2 Analytical approaches

We took two approaches to investigate mortality dynamics in the three plots: (1) individual-based regression models, to predict mortality from a suite of explanatory variables and (2) spatial point process analyses to characterise the spatial locations of living vs. dead trees. We also summarized characteristics of dead trees based on the field assessments. As our primary interest was differences in mortality patterns and processes between *N. fusca* and *N. menziesii*, analyses were undertaken separately for each species.

4.2.3 Individual-based mortality models

Models of individual-tree mortality were constructed using plot data spanning the 2001–2009 period. We parameterised a model describing the annual survival probability for each tree (similar to Lines et al., 2010) accounting for the slightly different periods, *t*, of the three plots through our study. The conventional approach to modeling tree mortality is to use logistic regression in a generalized linear modeling framework,

where the survival probability of each tree is modeled as a linear combination of explanatory variables, such as tree diameter and competition indices (Monserud, 1976; Hamilton, 1986; Yao et al., 2001). The response variable in our analysis is a vector indicating whether or not a tree has died (dead = 0, alive = 1). Assuming a constant annual survival rate for each tree through a census period of length *t*, the survival probability over *t*, *S*, for each tree expressed as a function of its annual survival rate, *s*, is:

$$S = (s)^t , \qquad \text{(equation 1)}$$

where *s* is formulated using a logit link function to map the probability of survival *S*, which has range [0, 1], onto the numerical range (–∞, ∞), and *k* is a linear combination of explanatory variables that could affect tree survival:

$$\log\left(\frac{s}{1-s}\right) = k . \qquad \text{(equation 2)}$$

Using the logit link function, the survival probability is:

$$S = \left(1 + \exp(-k)\right)^{-t} \qquad \text{(equation 3)}$$

We restricted individual-tree mortality analyses to deaths that occurred during the 2001–2009 census interval, so we could incorporate earlier data (i.e., 1986–2001) in the calculation of the explanatory variables that we hypothesized would influence the mortality risk for individual trees. Results reported graphically are shown in terms of annual mortality rate, *m*, (i.e. $m=1-s$).

Explanatory variables

Because mortality is often related to the size of an individual tree, we included initial tree diameter, *D,* from the beginning (2001) of the census interval. Because slow growth can reflect an increased risk of dying due to resource limitation (Bigler and Bugmann, 2003; Das et al., 2007) recent mean annual growth, *G*, was calculated for each focal tree based on diameter measurements made in 1986 and 2001. For each species we used a base model containing *D* and *G*, against which to assess the importance of additional variables. To capture the potential effects of neighbourhood competition on mortality, we incorporated two proxies for resource competition. To calculate the competition indices we used a circular neighbourhood with a radius of 20 m; support for this neighbourhood radius was provided by initial exploratory models that compared support for alternative radii in a model comparison framework using Akaike's Information Criterion (AIC). First, as a simple index of competition we summed the basal area of all larger neighbouring trees within 20 m of each focal tree (NCI_{simple}). Second, we used a more complex index of neighbourhood competition ($NCI_{complex}$) based upon traditional distance-dependent competition indices, that allow the effect of neighbouring trees on a focal tree to vary as a function of their size, and inversely to their distance from the focal tree (Canham et al., 2004). We used the Hegyi Index:

$$NCI_{Complex} = \sum_{j \neq 1} \frac{D_j}{D_i (d_{ij} + 1)} \qquad \text{(equation 4)}$$

where D_i is the diameter of the focal tree i, D_j is the diameter of each neighbouring tree within the 20-m radius of the focal tree, and d is the distance between focal (i) and neighbouring (j) trees. Both species display a strong positive relationship between tree diameter and height (i.e., large-diameter trees are usually tall trees; J.M. Hurst, unpublished data) which provides support for the use of competition indices based upon tree diameters, to approximate potential shading effects of neighbours (e.g., Monserud and Sterba, 1999; Yang et al., 2003). Competitive neighbourhood effects would be indicated by negative coefficients for NCI_{simple} and $NCI_{complex}$ in the models, whereas positive (or facilitative) effects of neighbours (e.g., Batista and Platt, 2003) would be indicated by positive coefficients. These analyses allowed us to address Hypothesis 1. To correct for edge effects for trees growing < 20 m from the edge of the plot, we adjusted all neighbourhood-based indices using an area-weighted edge-correction: index values were divided by the proportion of the neighbourhood contained inside plot boundaries (e.g., Das et al., 2008).

Because we were specifically interested in the degree to which mortality was contagious, that is, occurring near sites of previous mortality, we developed an index that categorized the local neighbourhood, for each focal tree, as either 'disturbed' or 'undisturbed'. The index was based on those developed by Coomes and Allen (2007) and Spence et al. (2011) and categorized neighbourhoods into developmental stages based on previous trends in basal area, stem density and mean stem diameter (i.e., in our case over the 1986–2001 period). Stands with declining basal area, stem density and mean stem diameter were classified as 'disturbed', distinguishing them from undisturbed stands (e.g., regenerating and thinning stands which typically did not

meet all of these criteria; Coomes and Allen, 2007; Spence et al., 2011). Comparison of mortality rates of trees with neighbourhoods classified as 'disturbed', or not, allowed us to address Hypothesis 2.

Finally, *Platypus* infestation may drive contagion in mortality, so we expected that *Platypus* infection of neighbouring trees would increase the risk of death for the more susceptible species, *N. fusca*. At each annual mortality census all living and recently dead trees (i.e., since the previous census) were examined for evidence of *Platypus* infection. These records were used to develop an index (*NP*) of *Platypus* infestation within each individual's neighbourhood, which indicated whether there were, or were not, trees infected within 5 m of each focal tree, during the 1986–2001 period, allowing us to address Hypothesis 4. We selected a neighbourhood size of 5 m based on evidence that most *Platypus* infection in managed stands occurs within 5 m of a previously infected tree (McCracken et al., 1994).

Model fitting and comparison

All continuous explanatory variables were standardized by subtracting the mean and dividing by two standard deviations so the regression coefficients allow each variable's effect size to be compared directly (Gelman, 2008). The explanatory variables, and interactions between them, were used to define a set of nine 'candidate models' (Burnham and Anderson, 2002). For each species, we first fit the candidate models to the entire sample of trees, but because the factors that predispose trees to mortality are likely to differ between small and large canopy trees (Coomes et al.,

2003), for each species we also fit the candidate models separately to 'small' (D < 15 cm) and 'large' ($D \geq 15$ cm) diameter trees. In addition, the candidate model set included models with interactions between tree size, D, and other explanatory variables. We examined support for each model in the candidate set using the small-sample version of Akaike's Information Criterion (AIC), along with the associated 'Akaike weights' (w_i). AIC works by balancing goodness of fit versus the number of parameters included in a model, where models with the smallest AIC values are those most strongly supported by the data (Burnham and Anderson, 2002). Each Akaike weight, w_i, describes the probability, given the data, of each model being the best in the candidate model set. To evaluate relationships between explanatory variables and mortality rate, model coefficients and variances were averaged across models based upon each model's Akaike weight, w_i (Burnham and Anderson, 2002). To ensure that our regressions were not influenced by colinearity amongst explanatory variables, we calculated Variance Inflation Factors (VIF) for each combination of variables. A conservative approach is to only fit combinations of variables that have VIFs < 3.0 (Zuur et al., 2010). In our models VIF was always <2.5.

4.2.4 Spatial point process summaries

Our second approach examined the spatial patterns of tree mortality using techniques developed for the analysis of spatial point pattern processes (Perry et al., 2006; Law et al., 2009). These analyses were restricted to the Station Creek plot, since it was fully mapped when established, so the location of every individual was known over

the entire 1986–2009 period (Figure 4.1). There was no topographic heterogeneity or obvious stand structure trends across the plot, so we employed methods for homogenous point patterns (Diggle, 2003). As done previously for the individual-based mortality models, we split data into 'small' (D < 15 cm) and 'large' ($D \geq 15$ cm) diameter trees for these analyses.

The spatial location of each tree and their survivorship form 'marked' point patterns, with marks being 'dead' or 'alive' based on a tree's fate during the 1986–2009 interval. Interpretation of mortality processes based on the spatial distributions of dead trees is not straightforward, as spatial patterns of dead trees are obviously contingent on the spatial pattern of all trees *before* any died (e.g., Moravie and Robert, 2003). We used a null hypothesis of 'random labeling' where the marks 'dead' and 'alive' were randomly reassigned to trees, while keeping the tree-locations fixed, as our null model (Goreaud and Pelissier, 2003). We compared the observed patterns to 999 simulations of the null model, to examine (1) aggregation of tree mortality events, and (2) patterns of spatial association between living and dead trees.

To examine whether dead trees were aggregated we used the univariate pair correlation function, $g(r)$, to summarise the spatial pattern of dead trees. The pair correlation function is the expected density of points in a ring, radius r centered on an arbitrary point, divided by the intensity of the pattern, λ (Stoyan and Penttinen, 2000); values of $g(r) < 1$ indicate regularity, $g(r) = 1$ randomness, and $g(r) > 1$ aggregation. These analyses allow us to examine whether the pattern of dead trees exhibited a spatial pattern, conditional on the locations of all pre-mortality living and dead trees as the null

model (e.g., Kenkel, 1988; Raventos et al., 2010; Yu et al., 2009). When summary function values from the observed data fell above the simulation envelope this indicated aggregation of dead trees at distance *r*, while summary function values below the simulation envelope indicated that dead trees are spatially more regularly distributed than expected at distance *r*, allowing us to address Hypothesis 3.

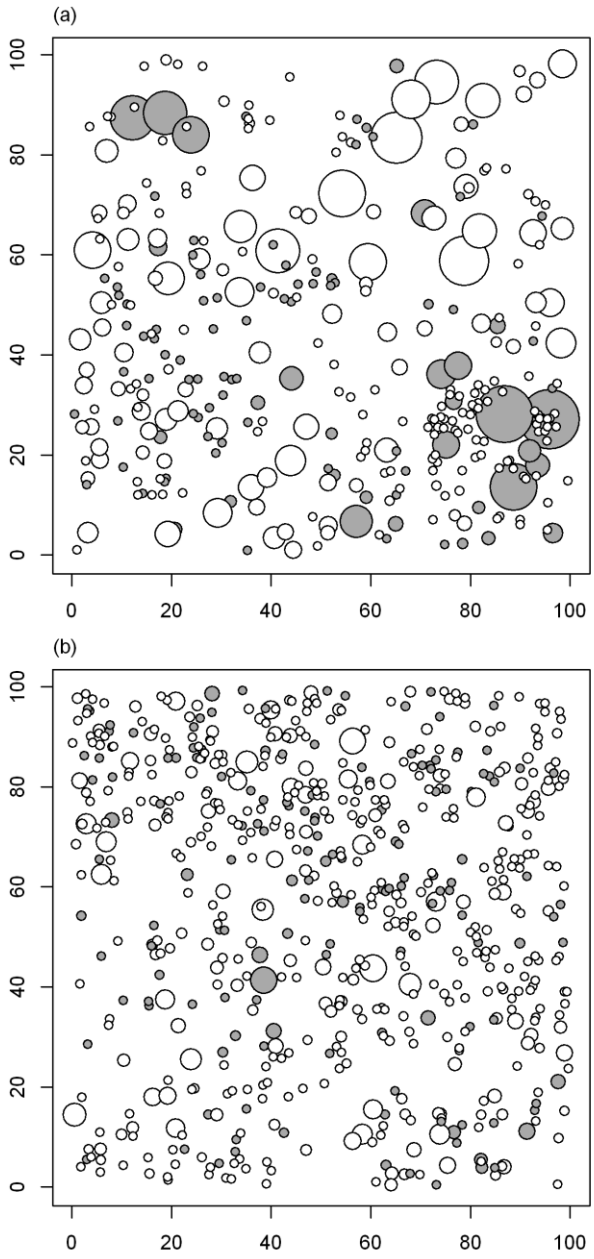

Figure 4.1. Map of the Station Creek stand used for point process analyses. Symbols represent dead (grey) and living (open) trees of (a) *Nothofagus fusca* and (b) *N. menziesii*. Each point is centred on the tree's location within the 100 × 100 m plot. The range of tree diameters is 5–190 cm for *N. fusca* and 5–80 cm for *N. menziesii*. Symbol sizes for large trees ($D \geq 15$ cm) are proportional to diameter, D. Symbols for small trees ($D < 15$ cm) correspond to those of a 15-cm-diameter tree.

To determine whether there was attraction or segregation between living and dead trees we used the bivariate pair correlation function, $g_{12}(r)$, as the summary function. This function describes spatial relationships between two types of marked points, e.g., the expected density of type 2 (e.g., dead) points, in a ring, radius *r*, centered on an arbitrary type 1 (e.g., alive) point, divided by the intensity of type 2 (e.g., dead) points, λ_2. If competition was a major source of tree mortality we would expect attraction (i.e. 'the [dead] "losers" in the contest being near its [surviving] rival'; Kenkel, 1988), rather than segregation, between living and dead trees. The bivariate summary function, $g_{12}(r)$, was also compared against a random labeling null model, $g_{1+2, 1+2}(r)$(e.g., Goreaud and Pelissier, 2003; Raventos et al., 2010). When summary function values from the observed data fell below the simulation envelope, this indicated segregation of dead and living trees (i.e., fewer living neighbours associated with dead trees at distance *r* than expected under random labeling), while summary functions above the simulation envelope indicated attraction of dead and alive trees (i.e., more living neighbours associated with dead trees at distance *r* than expected under random labeling). For both our univariate and bivariate pair correlation functions we used the Epanechnikov smoothing kernel with an isotropic edge correction as recommended by Stoyan and Stoyan (1994).

To assess the significance of each test performed, we used the null model simulations to generate an approximate 95% (two-sided) confidence interval, by determining, for each *r*, the 25th lowest and 25th highest value of the statistic from 999 simulations and the observed test statistic value. These envelopes can only loosely be interpreted as confidence intervals. Because the null model is simultaneously tested at

multiple scales, we also employ the Cranmer von Mises goodness-of-fit test (Loosmore and Ford, 2006) to avoid inflating the type I error rate. This test determines the rank, u_0, of the test statistic from the observed data relative to that calculated from simulations of the null model , and for a two-sided test the null model is rejected at the 5% significance level when $u_0 < 25$ or $u_0 > 975$. We performed all analyses in R *v.* 2.11.1 using the package spatstat (Baddeley and Turner, 2005).

4.3 Results

4.3.1 Mortality risk factors

Across the 2.7 ha encompassed by the three plots, 2749 *Nothofagus* trees were monitored across the 1986–2009 study period (1138 *N. fusca* and 1611 *N. menziesii*). Over the 2001–2009 period the overall mean annual mortality rate was nearly twice as high for *N. fusca* (0.016 $year^{-1}$) as for *N. menziesii* (0.0089 $year^{-1}$). Mortality of *N. fusca* was highest for the smallest trees (maximum rate 0.03 $year^{-1}$ for trees c. 5 cm *D*, Figure 4.2a), and lowest for the largest trees (minimum rate 0.005 $year^{-1}$ for trees > 100 cm *D*, Figure 4.2a). Across all tree diameters *N. menziesii* mortality was only weakly related to tree size (Figure 4.2a). When mortality of small (<15 cm *D*) and large (≥ 15 cm *D*) *N. fusca* and *N. menziesii* trees was considered separately, *D* was only an important predictor of mortality for large trees (Appendix 4.1, Table 4.2). Recent mean annual diameter growth, *G*, was a consistently important predictor of mortality risk for both *N. fusca* and *N. menziesii* (Figure 4.2b) both when all tree diameters were considered together and when small (<15 cm *D*) and large (≥15 cm *D*) trees were considered separately (Appendix 4.1, Table 4.2). Mortality risk for individuals of both species decreased with increasing growth rate (Figure 4.2b). The same analyses were repeated using relative growth rate as an explanatory variable, but this did not alter our results.

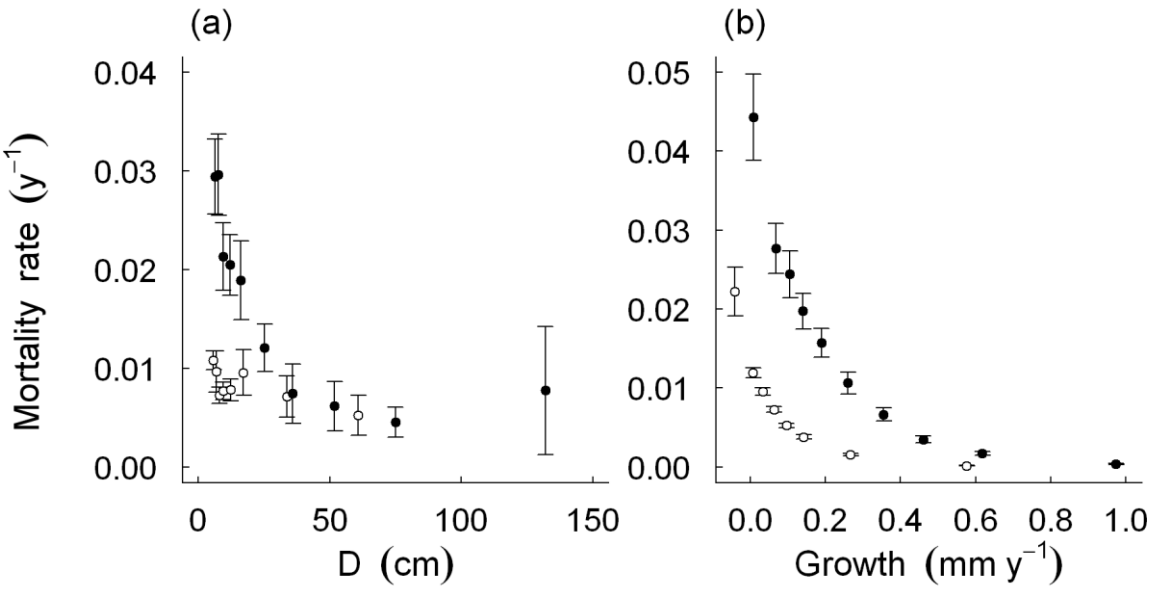

Figure 4.2. Mean mortality rate (year^{-1}; ±1.96 SE) against (a) tree diameter (*D*, cm), and (b) recent mean annual diameter growth (*G*, mm year^{-1}), for *Nothofagus fusca* (closed circles) and *N. menziesii* (open circles) over the 2001–2009 period, predicted using individual-based regressions. Each point represents a group of trees, binned by either diameter or growth, with 75 and 150 trees per bin for *N. fusca* and *N. menziesii* respectively.

For *N. fusca*, the distance dependent neighbourhood competition index ($NCI_{complex}$), that incorporated more information on the structure of each focal tree's neighbourhood, was a better predictor of mortality risk than a simple neighbourhood competition index (NCI_{simple}); the model including $NCI_{complex}$ (along with *D* and *G*) reduced AIC by five units, compared with the base model (e.g. a model that included only *D* and *G*; Table 4.1); though this model received little support (i.e., $w_i = 0.002$) compared with other models in the candidate set. $NCI_{complex}$ indicated neighbours had positive effects (i.e. negative regression coefficients) and reduced mortality risk, a result inconsistent with Hypothesis 1. Also, and contrary to Hypothesis 1, evidence for the importance of $NCI_{complex}$ varying with tree size, *D*, for *N. fusca* was weak (Table 4.1); AIC for the model that included an interaction between $NCI_{complex}$ and *D* was greater than the model without the interaction term, and was within 2.8 AIC units of the base model (Table 4.1). When mortalities of small (<15 cm *D*) and large (≥ 15 cm *D*) trees was considered separately, neighbourhood competition indices were consistently unimportant (Table 4.1).

For *N. menziesii*, there was no evidence that mortality risk was related to neighbourhood competition indices, neither when all tree diameters were considered together, nor when small (<15 cm *D*) and large (≥15 cm *D*) trees were considered separately; in all cases the AIC for the models including $NCI_{complex}$ and NCI_{simple} was greater than that of the base models (Table 4.1). Although models containing neighbourhood competition indices received some support (e.g., $\sum w_i = 0.156$ for small trees and $\sum w_i = 0.175$ for large trees), examination of regression coefficients for $NCI_{complex}$ and NCI_{simple} confirmed that they did not differ significantly from zero, a

result inconsistent with Hypothesis 1. For *N. menziesii* there was considerable model selection uncertainty for each set of candidate models considered, for example when all tree diameters were considered together three models had $w_i > 0.1$ and seven models had $\Delta AIC < 4$ (Table 4.1).

Stage of stand development was always an important predictor of *N. fusca* mortality, with the most supported models including the variable describing previous stand disturbance and reducing AIC by 5–17 units compared with the base models (Table 4.1). *N. fusca* trees in recently disturbed stands were more likely to die than those in undisturbed stands, indicated by a negative regression coefficient (Appendix 4.1, Table 4.2); and this strong effect of previous stand disturbance was consistent across both small (<15 cm *D*) and large (≥15 cm *D*) *N. fusca* (Table 4.1; Appendix 4.1, Table 4.2). Mean annual mortality of *N. fusca* growing in recently disturbed stands was more than twice that of other individuals (e.g., 0.0147 cf. 0.0056 per year). By contrast, for *N. menziesii*, mortality was no higher in previously disturbed stands than elsewhere, because AIC for models including '*Disturbed*' were always greater than or within two units of the base models (Table 4.1). These results support Hypothesis 2 for *N. fusca*, but not for *N. menziesii*.

Table 4.1. Akaike's Information Criterion (AIC) statistics for the candidate set of individual-based logistic regressions of *Nothofagus fusca* and *N. menziesii* tree mortality over the 2001–2009 period, fit across all tree diameters and separately for small (<15cm *D*) and large (≥15 cm *D*) trees. *D* = initial tree diameter, *G* = recent diameter growth, NCI_{simple} = basal area of larger neighbouring trees, $NCI_{complex}$ = Hegyi neighbourhood competition index, *NP* = *Platypus* presence/absence in 5-m neighbourhood around each tree, *Disturbed* = binary classification indicating previous disturbance. NCI_{simple} and $NCI_{complex}$ use a 20 -m radius to define neighbouring trees. K is the total number of estimated parameters in each model. ΔAIC is the difference in AIC between each model and the best supported model in the candidate set, with the best supported model having ΔAIC of zero. Model weights (w_i) indicate the probability of each model being the best in the candidate set, those with $w_i > 0.1$ highlighted in bold.

			All trees			Small trees			Large trees		
Species	Variables included	K	AIC	ΔAIC	wi	AIC	ΔAIC	wi	AIC	ΔAIC	wi
N. fusca	$D + G$	3	479.1	17.3	<0.001	269.0	12.2	0.002	203.4	5.0	0.047
	$D + G + NCI_{complex}$	4	473.9	12.1	0.002	270.9	14.1	0.001	204.7	6.3	0.025
	$D + G + NCI_{simple}$	4	479.9	18.1	<0.001	271.0	14.2	0.001	204.6	6.2	0.026
	$D + G + NP$	4	480.8	19.0	<0.001	271.0	14.2	0.001	205.1	6.7	0.020
	$D + G + Disturbed$	4	461.8	0	0.709	256.8	0	0.724	198.4	0	0.573
	$D + G + NCI_{complex} + D \times NCI_{complex}$	5	476.3	14.5	0.001	266.3	9.5	0.006	202.9	4.5	0.060
	$D + G + NCI_{simple} + D \times NCI_{simple}$	5	481.9	20.1	<0.001	272.6	15.8	<0.001	206.7	8.3	0.009
	$D + G + NP + D \times NP$	5	482.4	20.6	<0.001	273.3	16.5	<0.001	204.4	6.0	0.029
	$D + G + Disturbed + D \times Disturbed$	5	463.6	1.8	0.288	258.8	2.0	0.266	200.4	2.0	0.211
N. menziesii	$D + G$	3	480.2	1.4	0.177	366.5	0.9	0.212	119.6	1.2	0.115
	$D + G + NCI_{complex}$	4	482.3	3.5	0.062	368.5	2.9	0.078	120.9	2.5	0.081
	$D + G + NCI_{simple}$	4	481.7	2.9	0.083	368.5	2.9	0.078	120.6	2.2	0.094
	$D + G + NP$	4	478.8	0	0.356	365.6	0	0.333	121.1	2.7	0.073
	$D + G + Disturbed$	4	482.2	3.4	0.065	368.4	2.8	0.082	118.4	0	0.282
	$D + G + NCI_{complex} + D \times NCI_{complex}$	5	483.9	5.1	0.028	370.4	4.8	0.030	120.8	2.4	0.085
	$D + G + NCI_{simple} + D \times NCI_{simple}$	5	482.3	3.5	0.062	370.4	4.8	0.030	120.6	2.2	0.094
	$D + G + NP + D \times NP$	5	480.7	1.9	0.138	367.6	2.0	0.123	122.5	4.1	0.036
	$D + G + Disturbed + D \times Disturbed$	5	483.7	4.9	0.031	370.2	4.6	0.033	120.5	2.1	0.099

Platypus infection was frequently observed on recently dead trees. Significantly more dead *N. fusca* (31%) than dead *N. menziesii* (17%) displayed evidence of *Platypus* infection within a year of tree death (Chi-square test, $\chi^2 = 16.38$, $p \leq 0.001$). *Platypus*-infected trees in close proximity (i.e., within a 5-m neighbourhood) did not, however, increase mortality risk for *N. fusca* trees, with models including *NP* receiving little support (always $w_i < 0.02$, and higher AIC than the base models; Table 4.1), so Hypothesis 4 was not supported. In contrast for *N. menziesii*, when all tree diameters were considered together the best supported models in the candidate set included *NP* ($\sum w_i = 0.494$; Table 4.1). *N. menziesii* in close proximity to *Platypus*-infected trees were only marginally less likely to die (Appendix 4.1, Table 4.2): this is consistent with *N. menziesii* being relatively less susceptible to *Platypus* infection cf. *N. fusca*, and so, potentially, benefiting from canopy openings caused by *Platypus*.

Rates of *Platypus* infection tended to be higher for larger dead trees (infected trees had a mean *D* of 35.7 ± 4.4 cm (mean ± one SEM) and 22.1 ± 2.3 cm for *N. fusca* and *N. menziesii* respectively, compared with 12.9 ± 1.1 cm and 11.2 ± 0.6 cm for dead trees overall); *Platypus* infection was observed, however, across a wide range of tree sizes (from 5 to 230 cm *D* for *N. fusca* and 6 to 62 cm *D* for *N. menziesii*). Of those dead trees with evidence of *Platypus* infection 32% of *N. fusca* and 33% of *N. menziesii* were recorded as damaged in a previous mortality census, compared with just 9% surviving *N. fusca* and 10% surviving *N. menziesii* trees, an indication that damage was likely a risk factor leading to *Platypus* infection and tree death. At the first mortality census following tree death, the large majority of dead trees of both species were classified as 'standing with an intact crown' (71% and 62% for *N. fusca* and *N. menziesii*

respectively), followed by ‘standing with bole (main stem) broken’ (18% and 22%), ‘uprooted’ (2% and 7%), and ‘crushed by falling neighbouring trees or branches’ (9% for both species; see Appendix 4.1, Figure 4.5 for the spatial pattern of different tree death classes). Between species and across size classes (i.e. small vs. large trees) there were no significant differences in the proportions of dead trees in each category.

4.3.2 Spatial mortality patterns

The *g(r)* null model envelope for the pre-mortality pattern of small (< 15-cm *D*) *N. fusca* was greater than one at all distances (1–25 m), indicating that in 1986 small *N. fusca* were spatially aggregated over all distance scales (Figure 4.3a). By 2009, after accounting for this initial pre-mortality pattern of trees, dead small *N. fusca* were significantly ($u_0 = 1000$) more aggregated than expected under random labelling. This pattern was observed at a range of distances (e.g., 3–11 m, 15–17 m, 19–20 m, and 23 m; Figure 4.3a). For large (≥ 15 cm *D*) *N. fusca*, the *g(r)* null model envelope for all trees in 1986 was centered around one at all distances (1–25 m), indicating that in 1986 large *N. fusca* were randomly located (Figure 4.3b). By 2009, large dead *N. fusca* were significantly ($u_0 = 1000$) more aggregated than expected (e.g., at distances of 6–8 m and 13–23 m; Figure 4.3b), in support of Hypothesis 3.

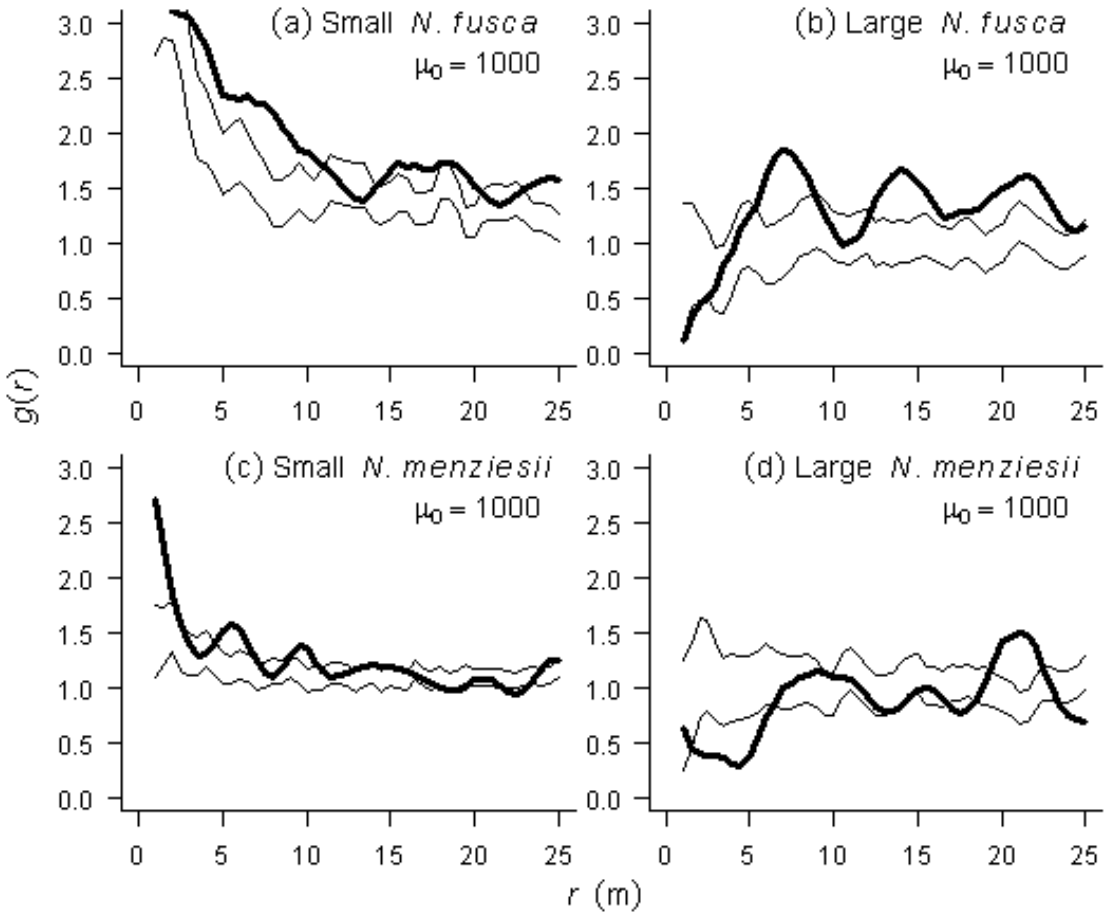

Figure 4.3. Univariate *g(r)* function for the observed pattern of dead trees (bold solid line), in relation to a random labeling null model (thin solid lines), for Station Creek over the 1986–2009 period: (a) small *Nothofagus fusca*, (b) large *N. fusca*, (c) small *N. menziesii*, (d) large *N. menziesii*. Small trees have diameter, $D < 15$ cm, and large trees have $D \geq 15$ cm. *g(r)* was calculated over 0 to 25 m and u_0 values ≥ 975 indicate that the observed pattern deviates significantly from the null model. Deviations of the observed pattern falling above the null model envelope indicate aggregation of dead trees at scale *r*, while deviations falling below the null model envelope indicate segregation (regularity) of dead trees at scale *r*.

For small (< 15 cm *D*) *N. menziesii*, the *g(r)* null model envelope for the pre-mortality spatial pattern also indicated spatial aggregation (Figure 4.3c), although this initial aggregation of small *N. menziesii* was less marked than that of small *N. fusca* (Figure 4.3a). By 2009, after accounting for this initial spatial pattern, small dead *N. menziesii* were significantly ($u_0 = 1000$) more aggregated than expected (at some distances < 11 m; Figure 4.3c), although *N. menziesii* mortality was regular at larger distances (e.g., *r* = 21–24 m; Figure 4.3c). As with *N. fusca*, the pre-mortality (i.e., 1986) pattern of all large (≥ 15 cm *D*) *N. menziesii* did not display spatial aggregation (Figure 4.3d). Although the spatial pattern observed for dead large *N. menziesii* deviated significantly from the null model ($u_0 = 1000$), there was no clear and consistent pattern. Instead, the observed spatial pattern of dead trees displayed a mix of regularity, randomness and aggregation (Figure 4.3d). Therefore Hypothesis 3 was not clearly supported for *N. menziesii.*

Small (< 15 cm *D*) living and dead *N. fusca* were significantly ($u_0 = 1000$) segregated as shown by the $g_{12}(r)$ summary function falling below the null model envelope (Figure 4.4a). This indicates that dead small *N. fusca* had fewer living neighbours than expected under random labelling, a pattern that was consistent across all scales examined (i.e., 1–25 m). A significant ($u_0 = 988$), but weaker pattern of segregation between living and dead trees was also observed for large (≥ 15-cm *D*) *N. fusca* trees (Figure 4.4b, e.g., at distances of 7–12 and 15–18 m). By contrast *N. menziesii* dead and living trees did not appear to be segregated: no significant pattern was detected for small ($u_0 = 873$, Figure 4.4c), or large trees ($u_0 = 833$, Figure 4.4d).

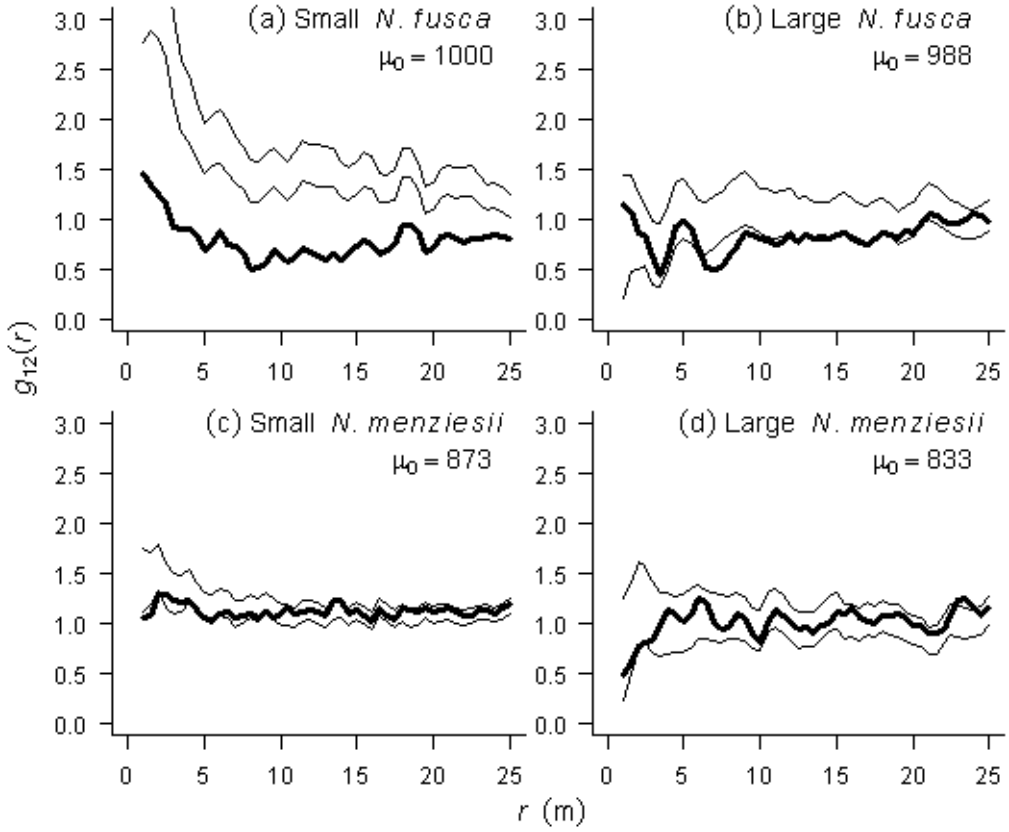

Figure 4.4. Bivariate $g_{12}(r)$ function for the observed pattern of dead and living trees (bold solid line), compared with the null model (thin solid lines), for Station Creek over the 1986–2009 period: (a) small *N. fusca*, (b) large *N. fusca*, (c) small *N. menziesii*, (d) large *N. menziesii*. Small trees have diameter, $D < 15$ cm, and large trees have $D \geq 15$ cm. $g_{12}(r)$ was calculated over 0 to 25 m and u_0 values ≥ 975 indicate that the observed pattern deviates significantly from the null model. Deviations of the observed pattern falling below the null model envelope indicate segregation of living and dead trees at scale *r*.

4.4 Discussion

4.4.1 Mortality risk factors

Because mortality patterns influence forest structure, composition and spatial arrangement of species and individuals, understanding the role of competition and disturbance processes as drivers of tree mortality is central to understanding forest dynamics (Oliver and Larson, 1990). Furthermore, knowing the relative importance of mortality risk factors for co-occurring tree species will allow us to develop predictive models of forest dynamics and to manage forest for timber production in a sustainable way. Our study showed that mortality was associated with different risk factors for the two congeneric study species, in part a reflection of different life-history traits such as shade-tolerance. For example, mortality was correlated with slow recent growth rates for both species, but for any given growth rate *N. fusca* was more likely to die than *N. menziesii*. Such a pattern could be generally expected for shade-intolerant vs. shade-tolerant species, since the latter are likely to better tolerate slow growth resulting from suppression; indeed previous studies corroborate this trend (e.g., Baraloto et al., 2005; Das et al., 2007; Kobe et al., 1995). Slow growth rates may, however, also reflect other abiotic or biotic stress factors, such as drought (Villalba and Veblen, 1998; Suarez et al., 2004), mechanical damage (Uriarte et al., 2004) and (susceptibility to) pathogens (Cherubini et al., 2002).

The strong size-related mortality that we observed for *N. fusca*, but not for *N. menziesii*, was also consistent with expectations for more shade-intolerant species. For example, with increasing tree size mortality rates of shade-intolerant species are

expected to decline because trees likely have increasingly greater access to light as they grow larger (Harcombe, 1987; Peet and Christensen, 1987). Given the strong size-related pattern, and the importance of recent growth for *N. fusca* mortality, we would normally expect mortality risk to be highest for those trees having greatest size-asymmetric competition with neighbours for light (e.g., Coomes et al., 2003; Hurst et al., 2011). We found no evidence, however, for an increase in *N. fusca* mortality with increased neighbourhood competition, a pattern inconsistent with Hypothesis 1. Instead, *N. fusca* mortality risk was highest for trees with initially fewer neighbours, while *N. menziesii* mortality risk was unrelated to neighbourhood competition. This result contrasts with many previous studies which emphasise the role of density dependent competition as a key mechanism driving tree mortality patterns in forests (Kenkel, 1988; Duncan, 1991; He and Duncan, 2000), though other studies also highlight that habitat suitability or various types of disturbance may modify spatial patterns of mortality (Gratzer and Rai, 2004; Greenwood and Weisburg, 2008; Yu et al., 2009). Our minimum tree size in this study was 5 cm diameter, and competitive processes may be more likely to play an important role in mortality for regenerating stems below this size (Ogden, 1988). Another explanation for a lack of important neighbourhood crowding effects in the present study is that the widely used competition indices (e.g. Hegyi Index and stand basal area) may not adequately represent the effects of neighbourhood crowding in these structurally complex old-growth forests that are subject to frequent natural disturbance. The competitive environment experienced by each individual tree is likely to vary considerably through time with the death or growth of neighbouring trees. Incorporating such variation when examining demographic rates

(e.g., Hartmann and Messier, 2011; Das et al., 2011), may enable better insights into the role of competition in such old-growth stands.

4.4.2 Spatial patterns of mortality

An alternative explanation for the lack of a correlation between neighbourhood competition and tree mortality is that in these old-growth stands competitive processes do not dominate tree mortality patterns. It may be generally true that in old-growth forests competitive processes are less important than they are in forests at younger stages of stand development (Franklin et al., 2002; Franklin and Van Pelt, 2004; Das et al., 2011). This suggestion is supported both by our individual-based analyses and by our examination of the spatial patterning of dead trees in the Station Creek plot. *N. fusca* mortality was most likely in areas that had been recently disturbed (i.e., those where basal area, stem density and mean stem diameter declined over the previous census period), a result consistent with Hypothesis 2. Our spatial analyses showed that mortality of both small and large *N. fusca* trees was aggregated over the 23-year period, and dead *N. fusca* were segregated from living trees, consistent with Hypothesis 3. In combination, these results suggest that mortality of *N. fusca* was spatially contagious across all size classes. Although our individual-based mortality models did not provide evidence that *Platypus* pinhole beetle infection of neighbouring trees increased *N. fusca* mortality, a result inconsistent with Hypothesis 4, we did find significantly higher infection rates of *Platypus* in *N. fusca* than in *N. menziesii*. The greater susceptibility of *N. fusca* to infection (McCracken et al., 1994) likely contributes to a pattern of

contagious mortality observed. By contrast *N. menziesii* dead trees were neither aggregated nor segregated from living trees.

4.4.3 Implications for forest dynamics and species coexistence

Because interspecific differences in mortality in part determine the relative performance of co-occurring tree species, our results have potentially important implications for forest dynamics and species coexistence. Together the contrasting spatial and size-related mortality patterns observed for *N. fusca* and *N. menziesii* indicate important performance differences for these two species in our study forest. For example, when considered alongside previous studies in mixed *Nothofagus* forest (e.g., Hosking and Kershaw, 1985; Ogden, 1988; Stewart and Rose, 1990), our study suggests that contagion in mortality of *N. fusca* should facilitate persistence of *N. fusca* populations in these old-growth forests. The density of *N. fusca* juveniles is usually greater than that of *N. menziesii* in the high light environments caused by large canopy gaps, so it is thought that canopy disturbances are likely to favor *N. fusca* regeneration (Stewart et al., 1991; Wiser et al., 2007). By contrast, for individual *N. menziesii* trees the mortality of neighbours is likely to be beneficial, as *N. menziesii* trees exhibit compensatory growth responses following canopy gap creation (Hosking and Kershaw, 1985; Wiser et al., 2005). Persistence of *N. menziesii* may also be afforded by lower mortality rates than *N. fusca*, over a wide range of diameter sizes. In summary, aggregated mortality of *N. fusca* trees should favor regeneration by this light-demanding species and perpetuate an aggregated distribution, whereas the lower, and more dispersed, mortality of *N. menziesii* trees allows a more widespread persistence.

Among tree species and across life stages, the balance between recruitment and mortality rate plays a key role in forest dynamics. In temperate mixed-species coniferous forests, Veblen (1986) considered that in *Abies lasiocarpa – Picea engelmannii* forest the greater recruitment of *Abies lasiocarpa* was balanced by greater loss of this species from the canopy through treefalls. Similarly, Hawkins and Henkel (2011) found that pathogens caused selective mortality of *Abies concolor* var. *lowiana*, which in turn favored persistence of *Pseudotsuga menziesii* var. *menziesii* through creation of canopy gaps for recruitment. It is important therefore to examine demographic performance, such as tree mortality rates, across multiple life stages to gain a comprehensive understanding of species coexistence (Nakashizuka, 2001). Further, our results suggest that we need to understand how spatial patterns of tree mortality differ among species. The spatial patterning of tree mortality events directly determines the size of canopy gaps that are created, which in turn influences the regeneration niches available for tree recruitment. Between species, different canopy-tree mortality patterns could therefore be as critical for species coexistence as the differences commonly observed at juvenile life stages (Kobe et al., 1995).

4.4.4 Sustainable forest management

Harvest regimes for managed *Nothofagus* forests are currently designed with the aim of mimicking natural disturbance regimes, for example by harvesting trees using small cuts with legislation restricting these to no more than 0.5 ha in *Nothofagus* forests (Ministry of Agriculture and Forestry, 2009). The use of small cuts and group selection

silvicultural systems has been of concern in New Zealand, due to the possibility of subsequent unintended mortality of residual canopy trees (Mason, 2000). Therefore it is important to compare demographic patterns in natural unmanaged forests with those in old-growth mixed *Nothofagus* forest managed for timber production. Wiser et al. (2005) studied the effects of small group selection harvesting (e.g., use of harvest cuts of 0.05–0.2 ha) on demographic rates in old-growth mixed-*Nothofagus* forest and found that over a 9-year period mortality of both *N. fusca* and *N. menziesii* was unrelated to harvest cut proximity. This result appears inconsistent with the contagious mortality we document for *N. fusca*, but harvested cuts in managed forest may differ from natural canopy gaps in a number of ways (Bengtsson et al., 2000; Schliemann and Bockheim, 2011). Timber is often carefully removed from harvested areas, and care is taken to avoid damaging adjacent trees; this may lead to lower mortality in residual trees than under natural conditions (Vasiliauskas, 2001). It should also be noted, however, that harvesting also includes removal of timber from the site, an activity that may lead to damage of residual trees causing subsequent mortality (Thorpe et al., 2008). Previous studies, although typically of limited duration, indicate large differences in the degree of post-harvest mortality (Jönsson et al., 2007; Thorpe and Thomas, 2007; Bladon et al., 2008). This may be due to variation in the amount of damage caused during the harvest operation.

The nature of compensatory growth responses of residual trees to harvested cuts depends both upon tree species and size. For example, Wiser et al. (2005) found that following harvesting, large *N. fusca* trees adjacent to cuts had slower diameter growth than similar sized trees in intact forest, but in their study these slower growing trees on

cut edges did not have higher mortality than those in intact forest; this may represent a decoupling of the growth–mortality relationship described in this study and others (e.g., Wyckoff and Clark, 2002; Wunder et al., 2007). Compensatory growth of trees adjacent to harvest cuts can also include increased lateral growth of canopy branches as well as increased diameter growth (Oliver and Larson, 1990). In relatively small harvest gaps this can result in fast gap closure (Splechtna and Gratzer, 2003) which in turn is likely to influence the regeneration patterns of *N. fusca* vs. *N. menziesii* (Wardle, 1984; Wiser et al., 2007).

Harvesting using small cut areas may therefore not necessarily mimic natural disturbance effects on tree mortality and growth. If mortality of *N. fusca* around small cuts is less contagious than in natural stands, this could potentially lead to longer-term changes in the relative abundance of *N. fusca* vs. *N. menziesii* in managed forests. This pattern might be exacerbated by the usually more uniform size and frequency of small-cut harvesting gaps compared to natural disturbance gaps. The results presented here clearly highlight the importance of having a sound understanding of ecological processes in natural stands, especially when the goal of forest management is to mimic natural disturbance regimes and sustain forest composition and structure (Lindenmayer and McCarthy, 2002).

Appendix 4.1. Supplementary data

Table 4.2. Coefficients of explanatory variables included in individual-based regressions for *Nothofagus fusca* and *N. menziesii*, for models fit for trees across all diameters and separately to small (<15 cm D) and large (≥15 cm D) trees. Model-averaging was used to estimate coefficients across the most supported models based upon the Akaike weights (wi; Burnham and Anderson, 2002; Johnson and Omland, 2004), using those models where wi.≥ 0.1.

Species	Variable	All trees	Small trees	Large trees
N. fusca	Intercept	5.181 (0.223)	4.617 (0.238)	5.666 (0.362)
	D	0.464 (0.366)	–0.211 (0.289)	1.056 (0.582)
	G	2.690 (0.430)	2.263 (0.404)	2.347 (0.526)
	Disturbed	–0.953 (0.229)	–1.068 (0.281)	–0.944 (0.378)
	D× *Disturbed*	0.081 (0.191)	0.006 (0.145)	0.011 (0.268)
N. menziesii	Intercept	5.071 (0.184)	4.859 (0.189)	6.211 (0.647)
	D	–0.418 (0.286)	0.030 (0.295)	–0.698 (0.545)
	G	2.741 (0.402)	1.750 (0.337)	3.831 (0.900)
	NP	0.467 (0.233)	0.353 (0.230)	
	D × *NP*	0.082 (0.164)	0.012 (0.123)	
	Disturbed			–0.622 (0.356)

Table 4.3. Continuous explanatory variables included in individual-based mortality models for *Nothofagus* spp.

	N. menziesii		*N. fusca*	
Explanatory variable	Median	Mean (± 1SE)	Median	Mean (± 1SE)
D (cm)	9.5	15.2 (4)	17.8	33.4 (1.3)
G (mm)	6.0	8.5 (3.6)	18.0	24.3 (8.0)
NCI_{simple}	64300	64131 (1187)	50109	49485 (1372)
$NCI_{complex}$	17.28	19.08 (0.36)	9.94	12.96 (0.39)

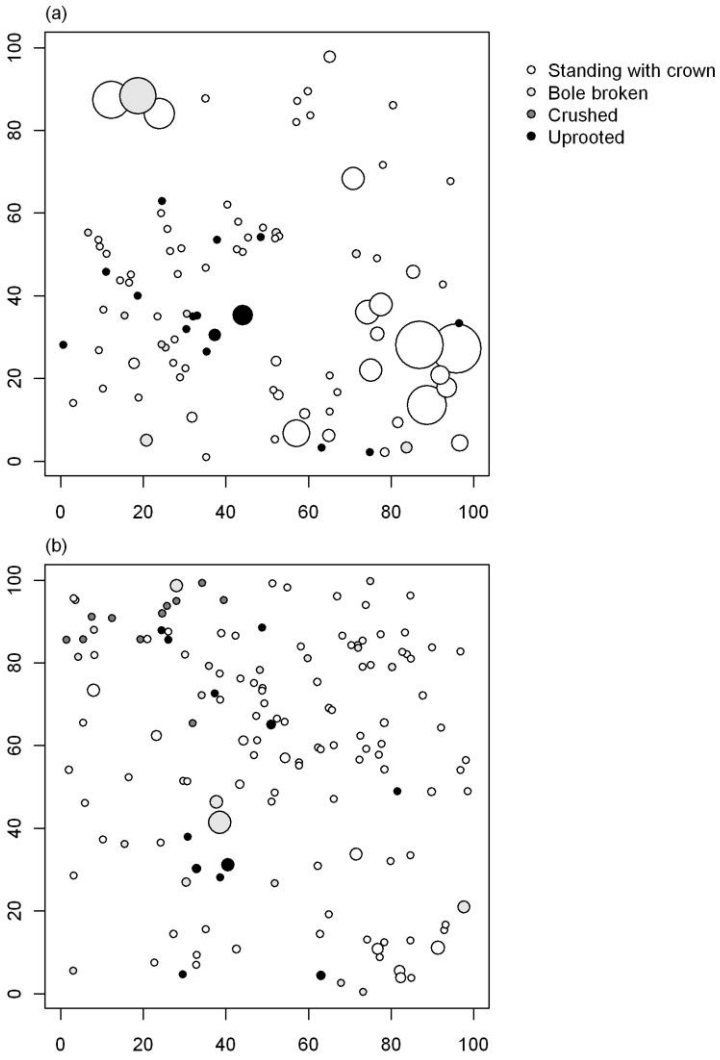

Figure 4.5. Map of the Station Creek stand used for point process analyses showing the spatial locations of different types of tree deaths for (a) *Nothofagus fusca* and (b) *N. menziesii*. Classifications of tree deaths were 'standing with an intact crown' (white), 'standing with bole broken' (light grey)', 'uprooted' (dark grey), and 'crushed by falling neighbouring trees or branches' (black). Each point is centred on the tree's location within the 100 × 100 m plot. The range of tree diameters is 5–230 cm for *N. fusca* and 5–80 cm for *N. menziesii.* Symbol sizes for large trees ($D \geq 15$ cm) are proportional to diameter, *D*. Symbols for small trees ($D < 15$ cm) correspond to those of a 15-cm-diameter tree.

Chapter 5 Simulated impacts of natural and harvesting disturbances on the composition and structure of mixed-*Nothofagus* forest

5.1 Introduction

Small-scale disturbances [2], whether natural or anthropogenic, influence the structure, composition, dynamics and stability of forests (Pickett and White, 1985; Franklin et al., 2002). An understanding of the impacts of small-scale disturbances is essential for sustainable forest management (Kunstler et al., 2013) and for tracking carbon sequestration and fluxes in forests (Vanderwel et al., 2013). The influence of small scale disturbances on forest dynamics and species dominance depends on their frequency, as well as their size and intensity (Runkle, 1985). Canopy gaps created by disturbance generally result in increased light available to seedlings or small trees (Canham et al., 1990) and create conditions favorable for recruitment, especially of shade-intolerant species which may otherwise decline in abundance through forest

[2] Defined here as perturbations causing the death of one or more canopy trees, creating canopy gaps, that typically vary in size from a few square meters to more than 1500 m^2, though usually they are less than 500 m^2 (Pickett and White, 1985; Runkle, 1985; Stewart and Rose, 1990; Stewart et al., 1991; Franklin et al., 2002).

succession (Pickett, 1980; Glitzenstein et al., 1986). Heterogeneity created by small scale disturbances can sometimes therefore promote the coexistence of multiple species in a forest (Denslow, 1985). Alternatively, small-scale disturbances could occur either so frequently or infrequently, that either pioneer or late-successional species might recruit, grow and survive best in the given conditions and become dominant (Denslow, 1980; Pickett and White, 1985; Glitzenstein et al., 1986; Shugart, 1987; Veblen, 1992). For surviving trees proximate to canopy gaps created by disturbance, growth and mortality may be either elevated or decreased, depending on species or tree size (Youngblood, 1991; Jones and Thomas, 2004; Wiser et al., 2005; Thorpe et al., 2008; Jones et al., 2009; Hurst et al., 2011). Overall, the course of forest dynamics following disturbance is determined by species-specific recruitment rates, and species and size-specific growth and mortality rates.

Because disturbance is prevalent in forests worldwide, numerous studies document the immediate impacts of natural or anthropogenic disturbance. This is useful on a site by site basis over relatively short timescales, but it is more difficult to examine the longer term consequences of disturbance because field data are often scarce. Forest dynamics simulation models allow examination of the long-term consequences of natural and anthropogenic disturbances on forest composition and structure (Coates et al., 2003; Thorpe et al., 2010). Modeling can be used to understand the consequences of new forest management systems that have not yet been empirically documented (Allen et al., 2012) and to compare long-term outcomes of different harvesting regimes (Coates et al., 2003; Arii et al., 2008). In structurally heterogeneous, mixed-species and mixed-aged forests, individual-tree based modeling approaches are most appropriate, as these

models are best able to represent the complex interplay between tree performance and local stand conditions (Peng, 2000; Coates et al., 2003).

In this study, a forest dynamics simulation model is used to explore the potential long-term consequences of various disturbance scenarios on the structure and composition of New Zealand mixed-*Nothofagus* forest. In these forests, shade-intolerant *N. fusca* is often the dominant canopy tree, but relatively shade-tolerant *N. menziesii* typically dominates the sub-canopy. It has been suggested that in the absence of major canopy disturbance, *N. menziesii* would eventually displace the more shade-intolerant *N. fusca* (Holloway, 1954; Wardle, 1984; Ogden, 1988), although both species appear to require canopy gaps for successful regeneration (Stewart and Rose, 1990). Management of mixed-*Nothofagus* forest for timber is controversial (Mason, 2000). Small-scale harvesting systems used in mixed-*Nothofagus* forest have a relatively short history of application, so long-term effects on stand structure and composition have not yet been assessed (Allen et al., 2012). Spatially explicit individual-based models have yet to be parameterised for mixed-*Nothofagus* forest, and matrix modeling approaches used previously are considered inadequate for examining the impacts of timber harvesting in these forests (Mason, 2000). By running simulations, I examine the influence of small-scale disturbance frequency on forest structure and composition. These simulations are then used as a baseline against which to assess the long-term outcomes of two alternate harvesting scenarios. In so doing the following questions are addressed:

1) How does variation in disturbance frequency influence long-term trends in forest composition and structure? A simulation was first run to represent the overall

'background' dynamics of these forests, primarily driven by the death of individual trees (i.e. in the absence of infrequent larger scale natural disturbance) and subsequent recruitment processes. Separate simulations were then run with varying frequencies of small-scale disturbance. With infrequent small-scale disturbance, *N. menziesii* is expected to increase in abundance, especially in large-tree size classes due to low large-tree mortality rates (Hurst et al., 2012). With frequent disturbance, shade-intolerant *N. fusca* is expected to increase in abundance in small-tree size classes because of high recruitment rates in canopy gaps (Stewart et al., 1991; Wiser et al., 2007), whilst declining in abundance in large tree size classes because of contagious *N. fusca* mortality patterns in disturbed stands (Hurst et al., 2012).

2) To what extent does timber harvesting influence long term forest composition and structure? This is addressed by simulating forest dynamics with two alternate timber harvesting scenarios. These impose harvesting at either a fixed or variable frequency, the latter simulation allowing an approximate basal area recovery interval to be estimated for mixed-*Nothofagus* forest.

5.2 Methods

5.2.1 Study Area

The simulation model was parameterised for low elevation old-growth mixed *Nothofagus* forest. Tree size-class structure at the three study sites used are broadly typical of mixed *Nothofagus* forests elsewhere in New Zealand, both species following

reverse-J shaped distributions with maximum diameters of *N. fusca* and *N. menziesii* ~190 cm and ~80 cm respectively. Elevation across the sites ranges from 450 to 600 m above sea level. Mean annual precipitation at nearby Springs Junction (425 m elevation, approximately equidistant to the three study plots) is 2280 mm, with > 130 mm recorded every month (National Institute of Water and Atmospheric Research, unpublished data). Mean annual temperature is 9.8°C, with a monthly minimum of 3.8°C (July) and monthly maximum of 15.2°C (January). Each site is located on relatively flat and fertile alluvial terraces. Valley-floor soils developed on Pleistocene glacial outwash deposits contain granite, greywacke, and schist (Bowen, 1964). These soils are acidic (mineral soil pH 4.0) with relatively high levels of available P.

Data from three long-term permanent research plots located at each of the three sites were used for model parameterisation (located at Pell Stream, Rough Creek and Station Creek). At the study plots *N. fusca* is most dominant in terms of total basal area (e.g., 58.0 $m^2 ha^{-1}$ vs. 14.4 $m^2 ha^{-1}$ for *N. menziesii*), but *N. menziesii* is dominant in stem density (529 stems ha^{-1} vs. 360 stems ha^{-1} for *N. fusca*). Each plot was 0.8–1.0 ha and was established in 1986, and fully remeasured in 2001 and 2009. During each measurement plots were subdivided into contiguous subplots of 5 × 5 m, within which all trees (DBH ≥ 5 cm) were uniquely tagged, identified and measured, and each tree was mapped and given an '*x*' and '*y*' coordinate (to within 0.5 m).

5.2.2 Model description and structure

Using the spatially-explicit permanent plot data described above, an individual-tree based simulation model was parameterised, and implemented in 'R' (R Core Team, 2012) using code specifically written for this study. The simulation model tracks the location of individual trees (≥ 5 cm DBH) across a hypothetical forest stand (1.96 ha in size). Individual tree recruitment, growth and mortality rates are estimated based upon features of the stand (e.g., neighbourhood basal area, recent disturbance) using relationships parameterised from the empirical data. By explicitly considering disturbance in the parameterisation of the growth and mortality sub-models (see Chapters 3 and 4), the simulation accounts for species-specific responses to the dynamic stand conditions created by small-scale disturbances. Each process included in the simulation model is described in further detail as follows.

5.2.3 Initial starting conditions

To initiate each simulation with a similar stand structure and composition to the mixed-*Nothofagus* forests in the study area, all simulations (aside from those described in section 5.2.9 'model evaluation' below), used 1.96 ha (140 × 140 m) stem maps that were generated from the permanent plot data. This larger stand size (compared to the individual plots) was chosen in order to minimise edge effects in the simulation, whilst still ensuring efficient processing time for each simulated stand. The starting conditions were generated by assembling together randomly selected 20 × 20 m areas from the 2001 data from the three permanent plots. To do this, a set of random x and y

coordinates for each plot were generated (n=16 for Rough Creek and Pell Stream and n=17 for Station Creek) and using the plot data the immediate 20 × 20 m area around each point was selected. These 20 × 20 m areas from all three plots were then joined at random to create a 1.96 ha composite stand. For each simulation this procedure results in unique starting conditions, whilst retaining features of the spatial structure of the sampled stands.

5.2.4 Recruitment

Tree recruitment is implemented in the simulations by estimating recruitment for each cell of a 5 × 5 m grid superimposed onto the simulated stand, based on analyses of tree recruitment into the ≥ 5 cm DBH size class on the mapped permanent plots. Using the periodic measurements of the permanent plots (i.e. measurements undertaken in 1986, 2001 and 2009), recruitment across the longest possible period (1986–2009) was analysed as a function of stand basal area in 2001. Analysis showed that shade intolerant *N. fusca* recruitment depended on stand basal area in the surrounding 15 × 15 m area (i.e. nine 5 × 5 m cells; see Appendix 5.1). The recruitment sub-model for *N. fusca* included an 8-year lag-effect based on this empirical data, which partially accounts for time taken for a tree seedling to reach the diameter threshold of 5 cm DBH (the minimum tree-size used in the simulation), though the tree seedling was likely to already exist in the pool of saplings (not included in the simulations). For example, for *N. fusca*, at each time-step, estimated recruitment of new stems is calculated based upon the total neighbourhood basal area eight years prior to that time-step. For *N. menziesii*, analyses of plot data showed that recruitment occurred independently of stand basal

area, so recruitment of *N. menziesii* was therefore set uniformly for each 5 × 5 m cell (see Appendix 5.1).

Recruitment rates were very low for both species and recruitment was always estimated at <1 new stem per 5 × 5 m cell per annum. To implement these low recruitment rates in the simulation, at each 1-year time-step a random number (range 0–1) was drawn for each cell using the *runif* function in R; if this was less than the estimated new stems recruited in that cell, then a new stem was recruited into the cell in the time-step. All newly recruited trees were assigned a diameter of 5 cm and a random location within the given 5 × 5 m cell.

5.2.5 Growth

The simulation makes use of species-specific relationships that estimate tree diameter growth (mm y^{-1}) as a function of features of the neighbourhood of each tree. These relationships were developed based on assessments of diameter growth of trees measured and mapped on the permanent plots (see Chapter 3) and utilise a traditional distance dependent measure of neighbourhood competition. This formulation assumes that large and proximate neighbours have the greatest competitive effects on trees and reduce their diameter growth (Weiskittel et al., 2011). For each individual tree, at each time-step, tree growth was estimated using the competition indices and parameters presented in Chapter 3. Analyses of the empirical data (Chapter 3) showed that *N. fusca* typically grew faster than *N. menziesii*, although *N. menziesii* exhibited strong compensatory growth responses when released from competition through the recent

death of neighbouring trees. This pattern was implemented in the simulation for each *N. menziesii* tree by keeping track of the location and timing of the death of any neighbouring trees, and using this to calculate a disturbance index for each *N. menziesii* individual at each time-step of the simulation.

5.2.6 Mortality

The parameterised mortality models for *N. fusca* and *N. menziesii* are based on relationships between mortality, recent growth and characteristics of a tree's neighbourhood. Relationships parameterised separately for each species (see Chapter 4, Hurst et al., 2012), were used to estimate individual tree mortality probability as a function of recent growth rate, neighbourhood competition and nearby disturbance. For each tree, at each time-step, neighbours within 20 m of each tree are identified, and a competition index calculated as outlined in Hurst et al. (2012). For *N. fusca* a disturbance index was also calculated, since the empirical data showed that *N. fusca* mortality rate was higher in areas with high previous disturbance (Chapter 4, Hurst et al., 2012). The probability (range 0–1) of each tree dying is then determined as a function of these indices. Using the *runif* function in R a random number (range 0–1) was drawn for each tree; if this was less than the estimated probability of mortality then the tree was killed in that time-step.

5.2.7 Disturbance

Disturbance was implemented to assess the effect of small-scale canopy disturbances on forest structure and composition. Separate scenarios were implemented using three alternate frequencies of disturbance ('low', 'intermediate' and high' frequency) and two alternate harvest disturbances (described below). A 'background forest dynamics' simulation was also implemented, in which no specific disturbance regime was imposed. This simulation has the least clustered pattern of tree mortality, as in this scenario the only disturbances are small gaps created through the death of individual trees.

The low, intermediate and high frequency disturbance rates were set at 0.01 gaps ha^{-1} $year^{-1}$ (i.e. destruction of one patch of trees per hectare every 100 years), 0.05 gaps ha^{-1} $year^{-1}$ (i.e. destruction of one patch of trees per hectare every 20 years) and 0.1 gaps ha^{-1} $year^{-1}$ (i.e. destruction of one patch of trees per hectare every 10 years) respectively. The intermediate disturbance rate is probably at the upper limit of small-scale disturbance events in the study area forests in recent decades. Stewart et al. (1991) sampled 150 gaps aged at 2–68 years, across a 47 ha area of mixed-*Nothofagus* forest; this is approximately equivalent to a disturbance rate of 0.046 gaps ha^{-1} $year^{-1}$ (i.e. assuming that all gaps <68 years old were identified).

For the 'low', 'intermediate' and 'high' frequency disturbance scenarios, disturbance was implemented by first randomly determining whether disturbance would occur based on the overall fixed frequency of canopy gaps per hectare per year. At each time-step when disturbance occurred, the location of the disturbance gap was assigned

randomly by selecting a point for the center of a circular expanded gap. An expanded gap (sensu Runkle, 1982) includes the canopy gap (i.e. the area delimited by vertically projecting the canopy opening to the ground surface) as well as the area surrounding this that extends to the bases of surrounding trees. Data from previous studies in mixed-*Nothofagus* forests was used to determine an appropriate range of sizes for the simulated small-scale canopy disturbance events; previous studies have shown that natural expanded gaps typically range in size from c.100–1000 m^2, with most falling in the range 200–400 m^2 (Stewart et al., 1991). By extrapolating from an existing size-class frequency distribution of gap sizes (Figure 5.1), mean expanded gap size was estimated at 369 m^2 (sd = 170 m^2). The size of each disturbance gap was assigned by drawing at random from a normal distribution with this mean and standard deviation, truncated at 100 m^2 and 1000 m^2 to be consistent with the canopy gaps sizes found by Stewart et al. (1991). Infrequent, larger-scale disturbance events such as earthquakes and catastrophic wind-throw may periodically cause larger natural canopy gaps in *Nothofagus* forest (Jane, 1985; Allen et al., 1999; Wells et al., 2001), but such events were not included in the simulations.

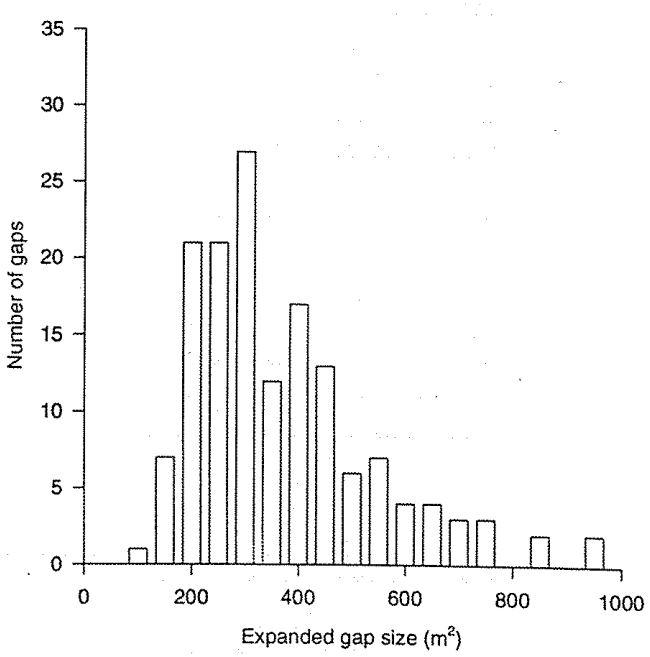

Figure 5.1. Size-class frequency distribution for expanded gaps at three localities in Maruia valley, North Westland, sampled by Stewart et al. (1991). The total area sampled was 47 ha. In total 150 expanded gaps were sampled; median expanded gap size was 295 m^2 (range of 91–939 m^2); median gap age was estimated at 20 years (range of 2–68 years; Stewart et al., 1991). By extrapolating from this size-class frequency distribution, the mean expanded gap size is estimated at 369 m^2 (sd = 170 m^2). Figure from Stewart et al. (2000).

Harvesting disturbance simulations

The provisions for timber harvest in New Zealand's mixed-species *Nothofagus* forests are implemented through Standards and Guidelines prescribed by Government (Ministry of Agriculture and Forestry, 2009). These were designed to reflect the natural disturbance regimes and dynamics of beech forests (e.g., Wardle, 1984) and are an attempt to perpetuate stands with mixtures of species and tree ages by using small-scale, low-impact harvesting systems (Benecke, 1996). In *Nothofagus* forest, harvested areas are restricted to ≤ 0.5 ha, unless approval is obtained for a larger area (Ministry of Agriculture and Forestry, 2009). However, in practice, in mixed-*Nothofagus* forest harvest regimes typically make use of small-group or small patch-cut selection systems, creating gaps 0.05–0.1 ha in size (Allen et al., 2012). Both *N. fusca* and *N. menziesii* are harvested and timber extraction is typically achieved through use of helicopters, although ground-based methods of timber extraction may be used at more accessible sites.

The two harvest simulation scenarios are simplified depictions of harvest systems that could be used in mixed-*Nothofagus* forest. In a sustainable management 'permit', as a starting point the standards and guidelines allow the removal of up to 10% of the basal area of a management unit within a ten-year period (Ministry of Agriculture and Forestry, 2009). In a sustainable management 'plan', up to 10% of the basal area of a management unit can also be harvested every ten years, but with the requirement that forest basal area must recover to pre-harvest levels before subsequent harvesting can occur (Ministry of Agriculture and Forestry, 2009). Two gap harvesting scenarios were

implemented to assess the suitability of these prescriptions; the first simulated harvesting 10% of the basal area of the stand every ten years (hereafter called the "High frequency harvest'), whilst the second simulated harvesting 10% of the basal area, at variable intervals such that basal area had recovered to pre-harvest levels before any subsequent harvest occurred (hereafter called the "Variable frequency harvest'). The following constraints were imposed in both harvesting scenarios. First, to ensure that harvesting in the simulation was targeted to merchantable trees (i.e. meeting a minimum diameter requirement), harvesting was only allowed in parts of the stand where there were >5 trees with diameter ≥30 cm, within 15 m. Second, to restrict the sizes of patch-cuts, simulated harvesting at any selected patch-cut in any year was restricted on average to 5% of the total stand basal area. In the high frequency harvest scenario, two new patch-cuts were simulated across the 1.96 ha stand every 10 years.

5.2.8 Model simulations

Simulations used a 1.96 ha stand generated as described above and ran for 500 years. For each of the six scenarios outlined above 50 simulations were performed so that variability amongst simulations could be determined. Variability arises from both the stochastic nature of the various sub-models implemented by the simulations, as well as variable starting conditions between runs. An example of variability in size structure and stem density across 50 starting condition stem maps is shown in Figure 5.2. Simulation results for each scenario and each species (*N. fusca* and *N. menziesii*) are

summarised by tabulating and graphing trends over time in basal area, stem density and size class structure.

5.2.9 Model evaluation

The very nature of simulating forest dynamics across long time periods makes it difficult to evaluate results against field data; field data are rarely available for long time periods, especially relative to the potential life-span of canopy tree species. The model was evaluated using quantitative comparisons with the short-term plot data used for model development. To assess the goodness of fit for the simulation results against the plot data, simulations were run for eight years using the three 0.8–1.0 ha study plots, corresponding to the 2001–2009 measurement period for each plot. Comparing the model with this validation data over a longer time period (i.e. starting in 1986) was not possible because the growth and mortality sub-models made use of stand disturbances in the prior period (i.e. 1986–2001) to determine the individual-tree growth and mortality rates. For each plot, simulation runs were repeated 50 times using the same starting conditions (i.e. plot data from 2001) to account for the stochastic nature of the model. Across the 50 simulations performed for each plot, minimum and maximum number of stems of each species in size classes and total basal area and stem density of each species were compared to the actual plot data from 2009 (see Figures 5.8 and 5.9, Appendix 5.2).

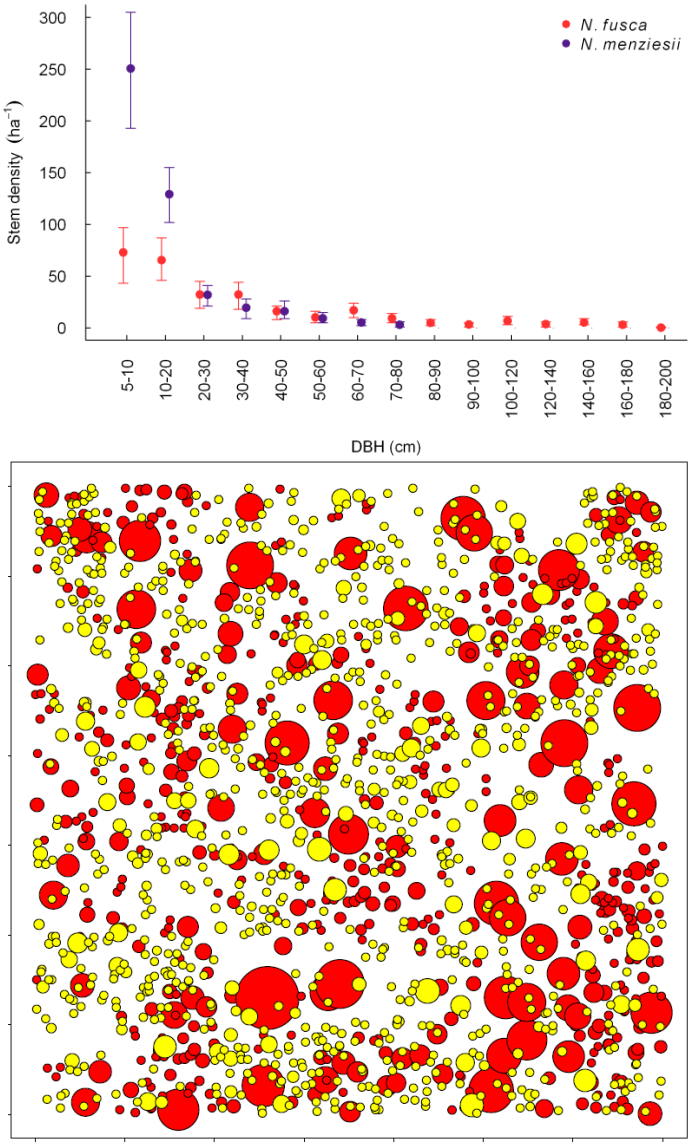

Figure 5.2. A. Size-class structiure for 50 starting condition stands generated randomly from permanent plot data, for *N. fusca* (red) and *N. menziesii* (purple). Points show mean stem density per hectare, and error bars show the minimum and maximum stem density in each size class across 50 generated stands. B. Example stem map for the starting conditions. Symbols represent *N. fusca* (red) and *N. menziesii* (yellow). Each point is centred on the tree's location within the 1.96 ha (140 × 140 m) plot. Symbol sizes for large trees ($D \geq 15$ cm) are proportional to tree diameter. Symbols for small trees ($D < 15$ cm) correspond to those of a 15-cm-diameter tree.

5.3 Results

5.3.1 Short-term model evaluation

Simulations run for eight years using the three 0.8–1.0 ha study plots (corresponding to the 2001–2009 measurement period for each plot) provided confidence in the model. Total basal area and stem density in 2009 were within the range given by 50 runs of the simulation, for all three plots and for both *N. fusca* and *N. menziesii* (Appendix 5.2, Figure 5.8). Size-class structures of both species also appeared to be acceptable over most size classes, with the exception being a poor fit for the 5–10 cm diameter size class for *N. fusca* at Station creek and *N. menziesii* at Rough Creek (Appendix 5.2, Figure 5.9).

5.3.2 Starting conditions

The stands used for initialising the simulations were dominated by large *N. fusca*, with a sub-canopy dominated by *N. menziesii* (Figure 5.2). The mean basal area was 69.2 (±0.5 SEM) $m^2\ ha^{-1}$, on average approximately 80% of which was *N. fusca* (54.9 $m^2\ ha^{-1}$ *cf.* 14.2 $m^2\ ha^{-1}$ for *N. menziesii*). Mean total stem density was 748 (±4 SEM) stems ha^{-1}, on average more than 60% of which were *N. menziesii* (465 stems ha^{-1} cf. 284 stems ha^{-1} for *N. fusca*). The size-class structure of 50 initial starting conditions is shown in Figure 5.2A. Small size classes comprised mainly *N. menziesii* (e.g., 5–20 cm; Figure 5.2A), while large tree size classes were dominated by *N. fusca* (Figure 5.2A).

5.3.3 Background forest dynamics

Simulation of the background forest dynamics (i.e. with no additional small-scale disturbance imposed) resulted in a strong compositional shift towards dominance by *N. menziesii*. After 500 years *N. menziesii* was dominant in terms of both basal area (increasing three-fold from 14.2 m^2 ha^{-1} to 45.8 m^2 ha^{-1}; see Figure 5.3A) and stem density (increasing from 465 stems ha^{-1} to 639 stems ha^{-1}; see Figure 5.4A). Conversely, *N. fusca* basal area declined over the 500-year period (from 54.9 m^2 ha^{-1} to 22.0 m^2 ha^{-1}; see Figure 5.3A), as did *N. fusca* stem density (from 284 stems ha^{-1} to 149 stems ha^{-1}; see Figure 5.4A).

Compared with the starting conditions, the resulting size class structures after 500 years indicated there had been a strong shift towards more intermediate sized *N. menziesii* (e.g., ~10–50 cm DBH; Figure 5.2A cf. Figure 5.5A). By contrast, the size class structure of *N. fusca* after 500 years comprised very few intermediate or large stems and a greater proportion of small trees (e.g., < 10 cm DBH; Figure 5.5A). Simulation runs of longer duration (e.g. >1000 years, not shown) indicated a continuing trend towards increased *N. menziesii* dominance.

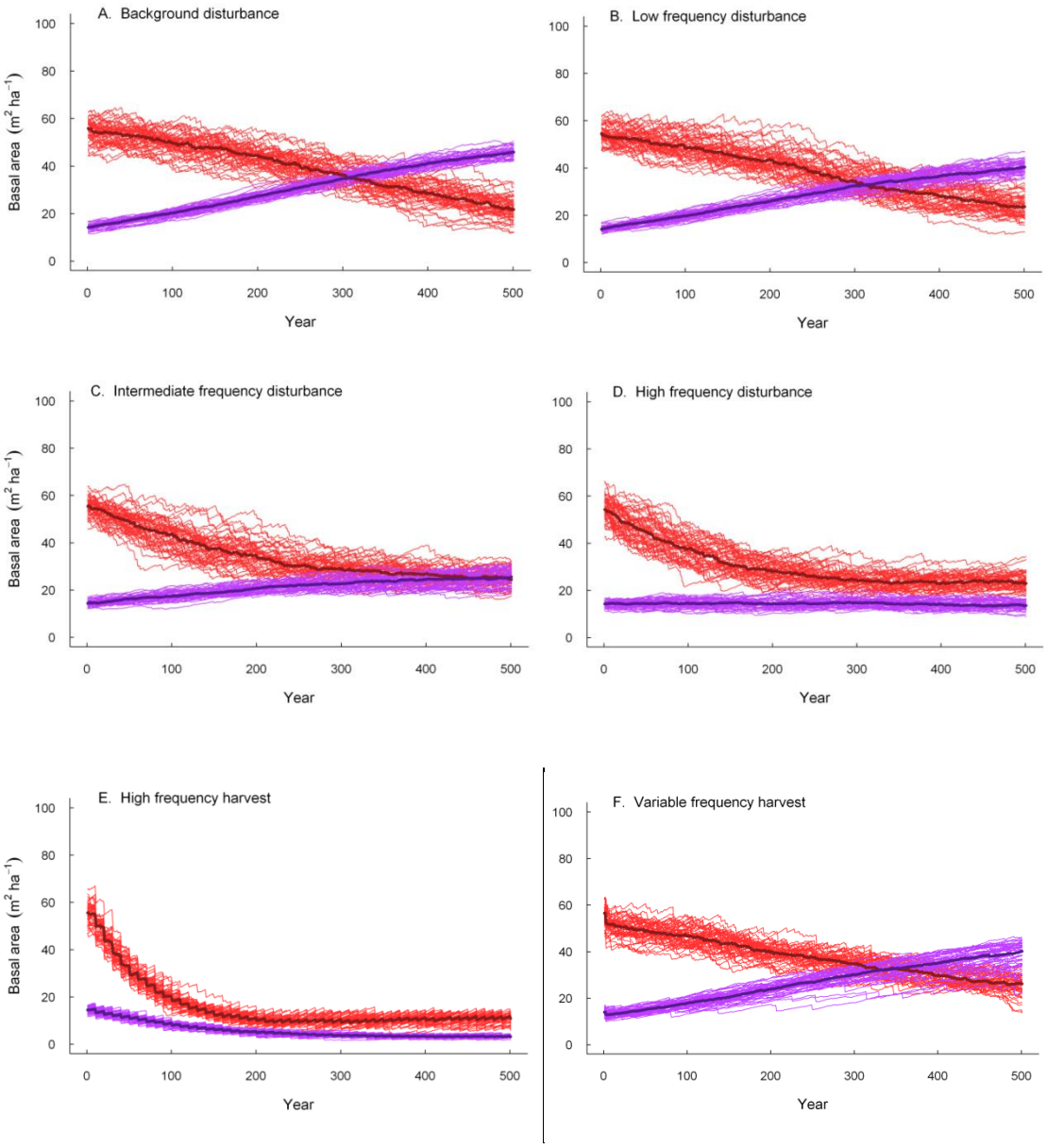

Figure 5.3. Trends in basal area ($m^2\,ha^{-1}$) over 50 simulation runs of 500 years, for *N. fusca* (red) and *N. menziesii* (purple), under various disturbance scenarios: A. Background forest dynamics, B. Low frequency disturbance, C. Intermediate frequency disturbance, D. High frequency disturbance, E. High frequency harvest and F. Variable frequency harvest. Each line represents one simulation run, with the darker lines showing the median trend for each species over all 50 simulation runs.

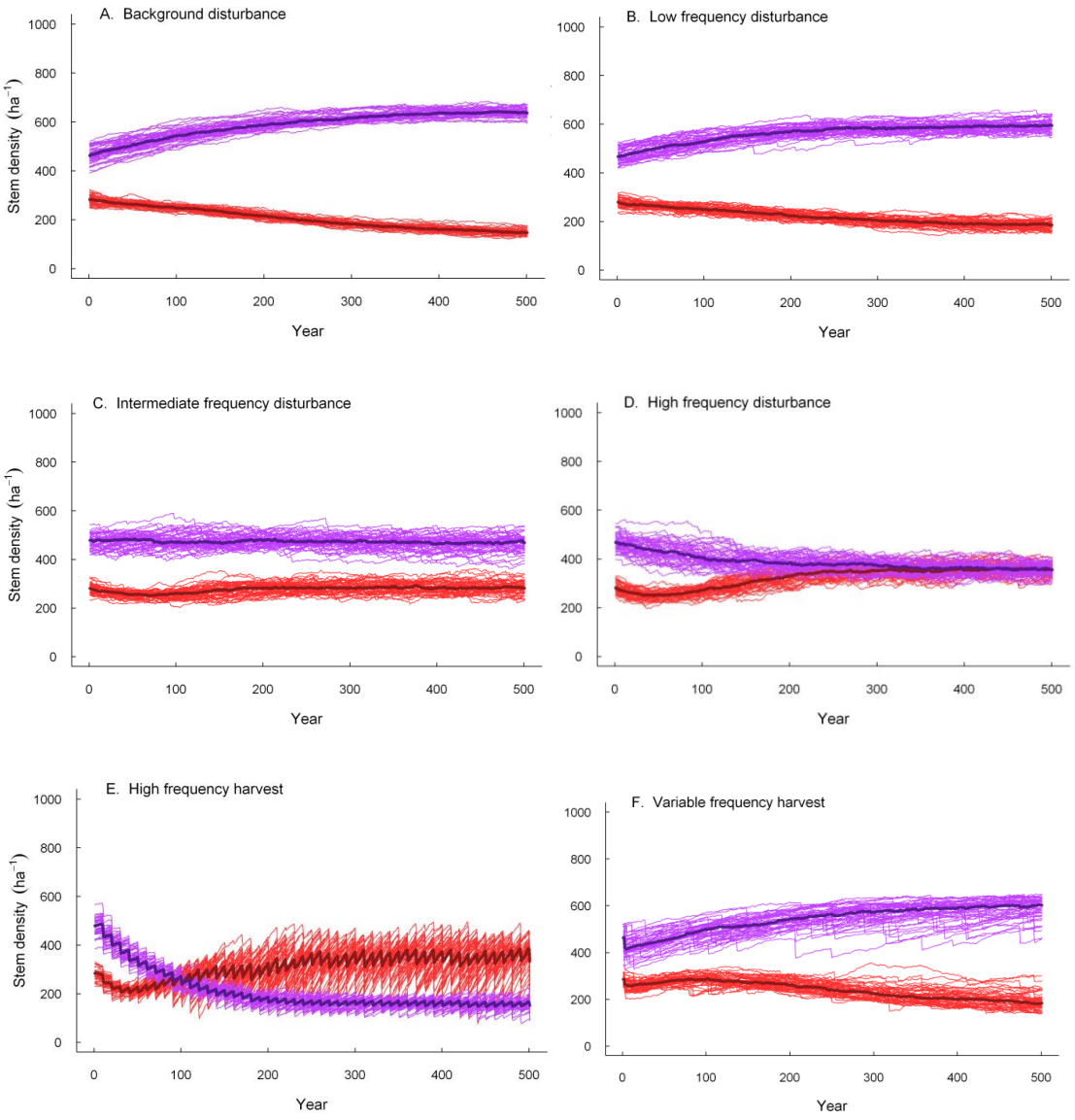

Figure 5.4. Trends in total stem density (stems ha^{-1}) over 50 simulation runs of 500 years, for *N. fusca* (red) and *N. menziesii* (purple), under various disturbance scenarios: A. Background forest dynamics, B. Low frequency disturbance, C. Intermediate frequency disturbance, D. High frequency disturbance, E. High frequency harvest and F. Variable frequency harvest. Each line represents one simulation run, with the darker lines showing the median trend for each species over all 50 simulation runs.

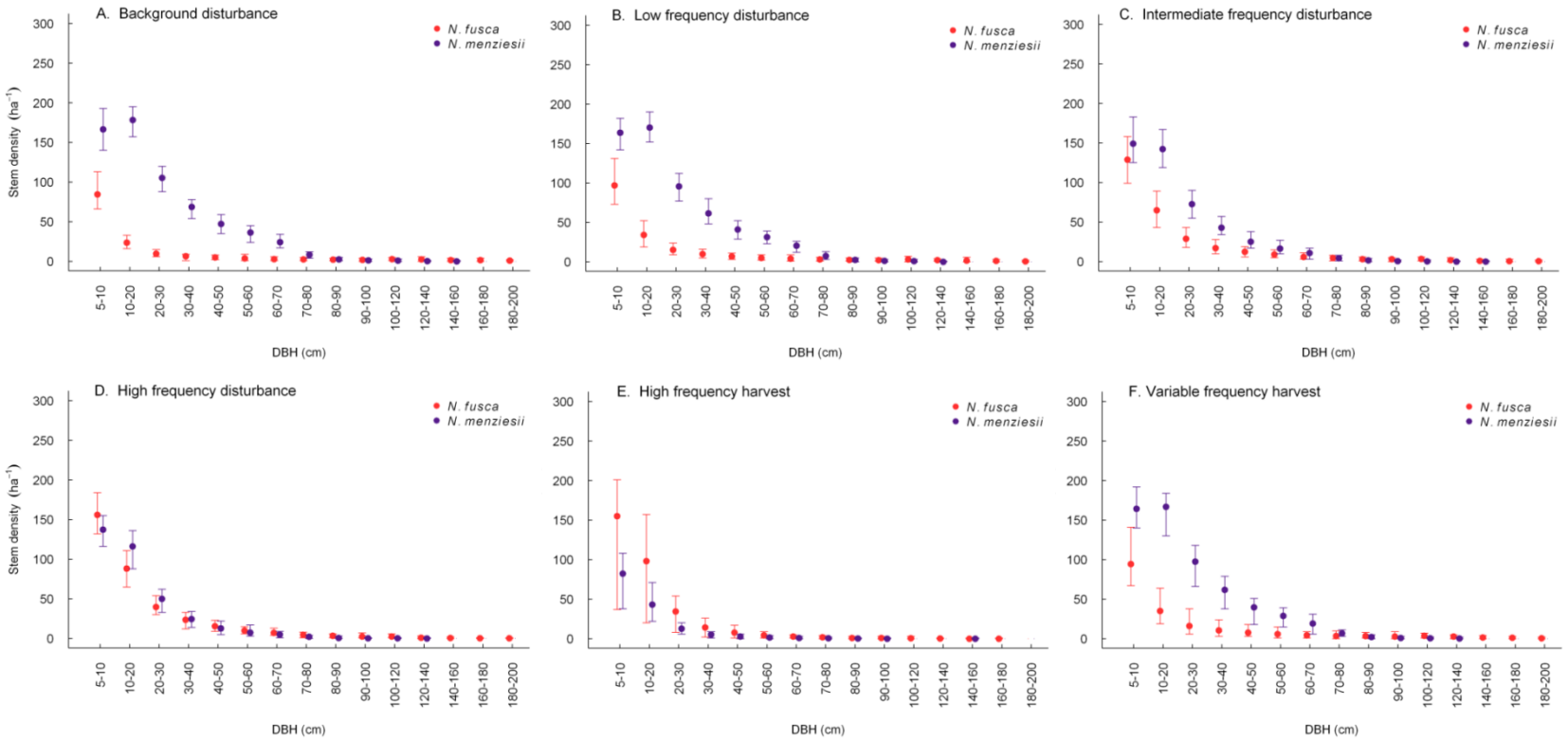

Figure 5.5. Simulated stand size-class structure after 500 years for *N. fusca* (red) and *N. menziesii* (purple), under various disturbance scenarios: A. Background forest dynamics, B. Low frequency disturbance, C. Intermediate frequency disturbance, D. High frequency disturbance, E. High frequency harvest and F. Variable frequency harvest. Points show the mean number of stems and error bars show the minimum and maximum number of stems, in each size class across 50 simulation runs.

5.3.4 Disturbance frequency

Low frequency disturbance promoted increased dominance of *N. menziesii*, in terms of basal area, while high frequency disturbance promoted dominance of *N. fusca*. After 500 years, for example, the low frequency disturbance scenario resulted in basal area (Figures 5.3A and B), stem density (Figures 5.4A and B) and size-class structure (Figures 5.5A and B) very similar to the background forest dynamics scenario described above, with *N. menziesii* dominant in terms of both basal area and stem density (Figures 5.3B and 5.4B). In contrast, under high frequency disturbance (i.e. destruction of one patch of trees per hectare every 10 years) *N. fusca* remained dominant in terms of basal area, throughout the simulated 500-year period (Figure 5.3D), although after 500 years the stem density of *N. fusca* and *N. menziesii* were approximately equal (Figure 5.4D).

Resulting size-class structures after 500 years also varied with disturbance frequency. Compared with the initial conditions, low and intermediate frequency disturbance resulted in increased density of intermediate-sized *N. menziesii* (Figure 5.2 cf. Figure 5.5). Intermediate and high frequency disturbance resulted in a greater density of small *N. fusca* (e.g., <20 cm DBH; Figure 5.2 cf. Figure 5.5D), and lower density of large *N. fusca* (Figure 5.2 cf. 5.5D, 5.6D).

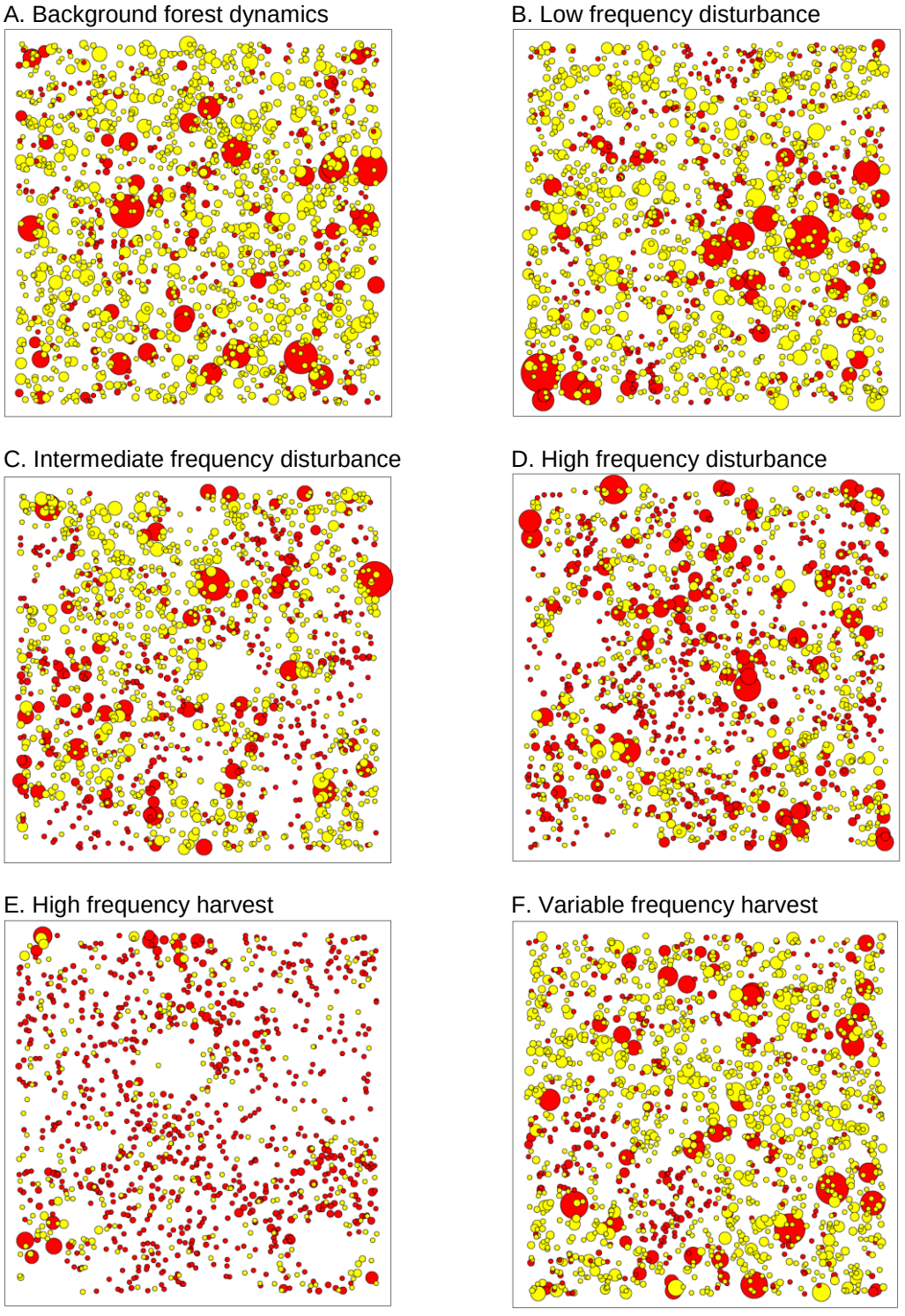

Figure 5.6. Examples of simulated stands after 500 years under each disturbance scenario: A. Background forest dynamics, B. Low frequency disturbance, C. Intermediate frequency disturbance, D. High frequency disturbance, E. High frequency harvest and F. Variable frequency harvest. Symbols represent *N. fusca* (red) and *N. menziesii* (yellow). Each point is centred on the tree's location within the 1.96 ha (140 × 140 m) plot. Symbol sizes for large trees ($D \geq 15$ cm) are proportional to tree diameter. Symbols for small trees ($D < 15$ cm) correspond to those of a 15-cm-diameter tree.

5.3.5 Harvest

Trends in basal area and stem density varied markedly between the two harvesting scenarios. Simulated high frequency harvest (i.e. 10% of basal area extracted every 10 years) led to basal area trends though time similar to the high frequency disturbance, but with overall much lower total basal area after 500 years (13.5 m^2ha^{-1} for harvest disturbance cf. 37.4 m^2ha^{-1} for the high frequency disturbance scenario; Figures 5.3D and 5.3E). Across the 500-year simulation patch cuts had a median size of 1407 m^2 (mean=2277 m^2, sd=2915 m^2). This is larger than the patch-cut sizes usually recommended in mixed-*Nothofagus* forest (Allen et al., 2012). *N. fusca* remained dominant in terms of basal area throughout the high frequency harvest simulation (Figure 5.3E). *N. fusca* stems became more common than *N. menziesii* stems after c. 100 years (Figure 5.4E) and this was the only simulation in which *N. fusca* stem density exceeded that of *N. menziesii* after 500 years (Figure 5.4E; on average 320 stems ha^{-1} for *N. fusca* cf. 148 stems ha^{-1} for *N. menziesii*).

For both species, the variable frequency disturbance scenario resulted in similar basal area and stem density trends to the low frequency disturbance scenario (Figure 5.3B and 5.3F). Two new patch-cuts were simulated across the 1.96 ha stand every 138 years on average (sd =88 years), with a median size of 1190 m^2 (mean=1363 m^2, sd=881 m^2, at the upper limit of patch-cut sizes usually recommended in mixed-*Nothofagus* forest).

5.4 Discussion

5.4.1 Background forest dynamics and disturbance frequency

Using a spatially explicit simulation model, this study demonstrated that in mixed-*Nothofagus* forest the frequency of small-scale disturbance over a 500-year period was a major determinant of forest composition and structure. Specifically, the frequency of small-scale disturbance determined whether conditions favoured dominance of *N. fusca* or *N. menziesii*. Small canopy gaps (for example, those created through death of individual trees in the background forest dynamics scenario) and low frequency disturbance (i.e. destruction of one patch of trees per hectare every 100 years) led to a forest dominated, in terms of both basal area and stem density, by *N. menziesii*. These results are consistent with the contention of Holloway (1954) who considered that in the absence of major disturbances, shade-tolerant *N. menziesii* would replace shade-intolerant *N. fusca.* Previous reconstruction of disturbance history and size and age class structures have indicated that even small trees of relatively shade-tolerant *N. menziesii* require release from competition in order to reach the canopy (Stewart and Rose, 1990). When disturbance is infrequent, increasing dominance of *N. menziesii* through time is therefore likely to be due to high initial dominance of *N. menziesii* in sub-canopy tiers, combined with individual tree deaths or small-scale disturbance that accelerate the transition to *N. menziesii* dominance due to compensatory growth responses by *N. menziesii* in trees growing close to canopy gaps (Wiser et al., 2005). Under more frequent canopy disturbance regimes, succession is interrupted and reinitiated, and relatively shade intolerant *N. fusca* increases in dominance.

5.4.2 Harvesting disturbance frequency

Silvicultural systems for mixed-*Nothofagus* forest were designed to mimic natural disturbance regimes and perpetuate mixed-species and mixed-aged stands using small-scale, low-impact harvesting systems (Benecke, 1996). Because such systems have only a short history of use in New Zealand, long term impacts have not been thoroughly tested (Allen et al., 2012). The simple representations of timber harvesting implemented in the simulations showed that harvest frequency has a large impact on long-term forest structure and composition. High frequency harvest resulted in major deviations away from the background forest dynamics trajectories, resulting in a forest dominated by relatively small *N. fusca* after c. 100 years. The high frequency harvest scenario does not appear to be congruent with other goals of New Zealand forestry legislation, such as the aim to achieve a balance between productive use of forest and maintenance of natural values (e.g., retention of a mixed age structure, maintenance of large trees, maintenance of stand composition; Ministry of Agriculture and Forestry, 2009). Intensive forest management for timber can homogenise stand structure and reduce structural complexity (Zenner, 2000). Although unmeasured in the present study, both vertical complexity in the forest canopy, as well as horizontal variation in stand density, are likely to be reduced under high harvesting regimes; over time this will result in reduced key habitat features such as large standing dead trees and coarse woody debris. Finally, both the high frequency harvest and high frequency disturbance scenarios had small-scale disturbances inflicted every ten years, with quite different resulting stand structure and composition. This indicates that the greater patch size, along with selectively targeting patches of large trees, likely contributes to the unsustainability of

high frequency harvest scenario which led to such a marked change in structure and composition.

With less frequent harvest imposed by the variable frequency harvest scenario, basal area, stem density and size structure were all similar to that of the background forest dynamics (where disturbance was restricted to individual tree deaths) and low frequency disturbance (one disturbance ~0.4 ha on average every 100 years) scenarios, with the forest becoming increasingly dominated by *N. menziesii* through time. This result implies that infrequent harvesting has only minimal effects on long-term trends in forest composition and structure.

Comparing the outcomes of variable frequency harvesting with the low frequency disturbance simulation may provide useful guidelines regarding an appropriate return interval for harvesting in mixed-*Nothofagus* forest. It should be noted however that both harvesting scenarios placed very few constraints on where harvesting could occur, the only requirement being the presence of merchantable trees (> 30 cm DBH) in the vicinity of the patch cut. An additional constraint imposed by legislation is that regeneration at a previously harvested patch cut must have reached a predominant height of 4 m, with a stocking of the harvested species equal to or greater than pre-harvest levels, before adjacent harvesting can occur. Such further constraints should be incorporated into future harvesting simulations. The variable harvesting frequency scenario also involved removing 10% of the total stand basal area at each harvest, regardless of the size of canopy gap that this would create. Patch-cut size determines whether conditions are more suitable for either *N. fusca* or *N. menziesii* recruitment

(Wiser et al., 2007), however the simulations did not examine the relative importance of harvest frequency versus patch-cut size on long-term structure and composition. It would be useful to adapt the harvesting algorithm to address these limitations.

5.4.3 Model evaluation

Conclusions based on forest simulation modeling always come with attendant caveats. Firstly, the simulation was parameterised using data from permanent plots where small-scale disturbance events influenced forest composition and structure over a 23-year period. It is unclear the extent to which the disturbance regime captured by the plot data represent average conditions for mixed-*Nothofagus* forests; further, it is unlikely that only smaller-scale disturbances would occur in mixed-*Nothofagus* forest over a 500 year period as depicted in these simulations. Many larger scale disturbance events are known to affect *Nothofagus* forests, such as drought and severe insect outbreaks causing dieback over large areas (e.g., Wardle and Allen, 1983; Hosking and Kershaw, 1985). In tectonically active regions, infrequent large earthquakes can also be a dominant factor driving the dynamics of forests (Veblen and Ashton, 1978; Wells et al., 2001). In New Zealand the legacy effects of large earthquakes on forest structure and composition have been demonstrated to last for decades or centuries (Vittoz et al., 2001; Wells et al., 2001; Cullen et al., 2003). Periodic regeneration in openings created by large disturbances such as earthquakes can lead to synchronous regeneration of cohorts of fast colonizing or fast growing species. Earthquake impacts in mixed-*Nothofagus* forests following a major earthquake were studied by Vittoz et al. (2001),

who found that whilst *N. fusca* tended to become more dominant than *N. menziesii* following earthquakes, earthquake impacts varied considerably amongst stands and resulted in heterogeneous patterns of forest structure and composition. Extrapolating the model to simulate the consequences of infrequent, larger-scale disturbances should be done with caution however, because model parameterisation was undertaken using data from a period characterised by small-scale disturbances.

The small-scale disturbance regimes implemented in these simulations were also simple, non-selective events that killed patches of trees regardless of tree species and tree size. In reality however natural disturbances probably only rarely cause the complete removal of existing trees in a disturbed patch (Franklin et al., 2002), whilst careful harvesting practices should also minimize damage to advance regeneration. Many of the disturbances affecting mixed-*Nothofagus* forests may be selective on certain species, tree sizes or sites. For example, *N. fusca* is more susceptible to some insect outbreaks and associated fungal pathogens (Hosking and Kershaw, 1985; McCracken, 1994), while larger or taller trees in many forests are most susceptible to wind-throw (Canham et al., 2001; Martin and Ogden, 2006). Further consideration should be given to the types and magnitude of disturbances implemented in the simulations. Where there is sufficient empirical evidence to support the size or species selectivity of disturbance, additional constraints on the simulations could be imposed.

Finally, evaluating the results of any long-term simulation model is difficult when only short term field data are available with which to compare simulation outcomes. When forest simulations are run for long time periods the propagation of errors due to

parameter uncertainty can be of concern (Deutschmann et al., 1999). The simulation runs appeared to perform adequately over a short 8-year period when compared against the parameterisation data providing confidence in the model. Ideally however, additional validation with independent data would also be undertaken (Astrup et al., 2008). Further model evaluation can help ascertain that the relationships modeled by each sub-model are not overly dataset specific (Astrup et al., 2008) and to check that the model can be generalized to mixed-*Nothofagus* forest over a wider geographic area. For each sub-model (i.e. recruitment, growth and mortality), the best supported parameterisation was selected for each species based on model selection criteria (e.g. AIC, Burnham and Anderson, 2002). This does not however provide certainty that the selected sub-model is best suited for simulating the dynamics of mixed *Nothofagus* stands. When suitable independent data are unavailable, sensitivity analysis is a useful technique that can reveal the model parameters that cause the greatest fluctuation in results when perturbed (Weiskittel et al., 2011). A formal sensitivity analysis to both the starting conditions, as well as to sub-model parameters is required (e.g., Pacala et al., 1996).

5.4.4 Conclusions

Forest simulation models allow the extrapolation from short-term observations to long-term examination of forest structure and composition under differing small-scale disturbance scenarios. This study demonstrates the potential of an individual-based forest simulation model for mixed-*Nothofagus* forest, for assessing the consequences of

small scale disturbances and harvesting on forest composition and structure. Disturbance frequency had a dramatic influence on forest composition and structure after 500 years, providing a framework against which forest management regimes can be assessed. Further work is needed to determine the sensitivity of model outcomes to model parameterisation, whilst the ability of the model to simulate dynamics of mixed-*Nothofagus* forests using independent data should also be tested.

Appendix 5.1 Recruitment analysis for use in simulation modelling

Recruitment of *N. fusca* and *N. menziesii* into the > 5 cm DBH size class was analysed as a function of neighbourhood basal area. Because recruitment rates are relatively low, and subject to temporal variability, this was done using the longest time-span possible in the data available from the three mapped plots (i.e. the 1986 to 2009 period). For each 5 × 5 m subplot, new recruits (>5cm DBH) in 2009 were identified and counted. Subplots with no new recruits were assigned a count of zero. Total neighbourhood basal area for 15 × 15 m area around each subplot was calculated in 1986 and 2001. All subplots located within 5 m of the edges of the plots were excluded from these analyses since for these subplots neighbourhood information was incomplete. For each species, the influence of basal area on recruitment was determined using AIC to compare alternate models.

The recruitment data was zero-inflated (i.e. the response variable contains more zeroes than expected based upon the Poisson or negative binomial error distributions; Zuur et al., 2009). One way to deal with zero-inflated data is to first model the probability of obtaining a zero sapling count, and then model the non-zero observations (e.g., see Zuur et al., 2009). Using Akaike's Information Criterion to compare support for negative binomial vs. Poisson error terms, models using the negative binomial distribution were found to be more supported for both species.

To determine whether basal area was an important explanatory variable, recruitment models were compared that used either basal area in 1986 or 2001 against a null model that did not include basal area as an explanatory variable. These analyses

showed that a model using the 2001 basal area was most strongly supported for *N. fusca* (e.g., ΔAIC=0; Table 5.1), with recruitment highest in cells with a low neighbourhood basal area (Figure 5.7). *N. menziesii* recruitment was unrelated to neighbourhood basal area, since both models including basal area were less supported than the null model (Table 5.1, Figure 5.7).

Table 5.1. Akaike's Information Criterion statistics for three alternative models fit to *N. fusca* and *N. menziesii* recruitment data. All models were fit using a zero-inflated model with a negative binomial error distribution. Selected models are highlighted in bold.

Species	**Model**	**AIC**	**ΔAIC**
N. fusca	Null	669.3	52.4
N. fusca	BA_{1986}	670.2	53.3
N. fusca	**BA_{2001}**	**616.9**	**0**
N. menziesii	**Null**	**740.2**	**0**
N. menziesii	BA_{1986}	743.8	3.5
N. menziesii	BA_{2001}	742.4	2.2

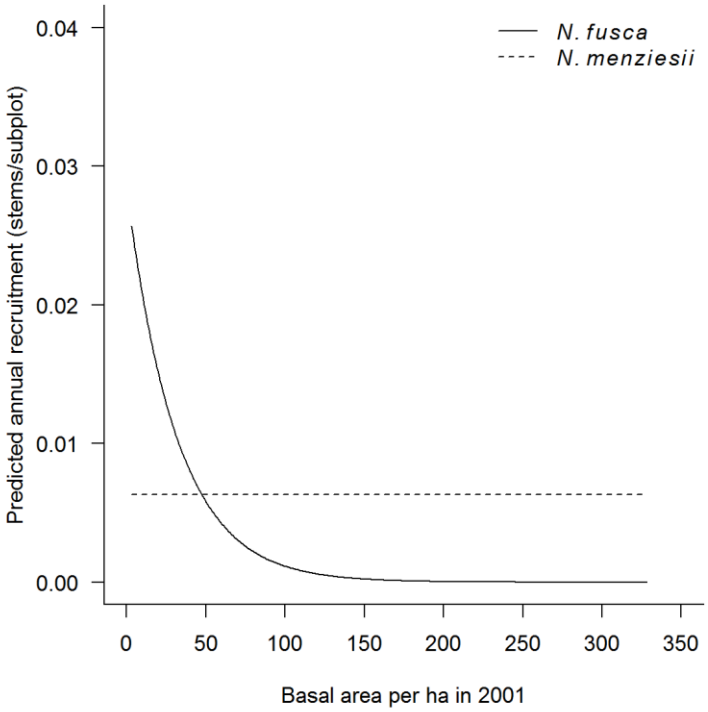

Figure 5.7. *N. fusca* (solid line) and *N. menziesii* (dashed line) annual recruitment (stems per 5 × 5 m cell) versus basal area ha^{-1}, based upon models fit to permanent plot data over the 1986–2009 period.

Appendix 5.2 Model evaluation using permanent plot data

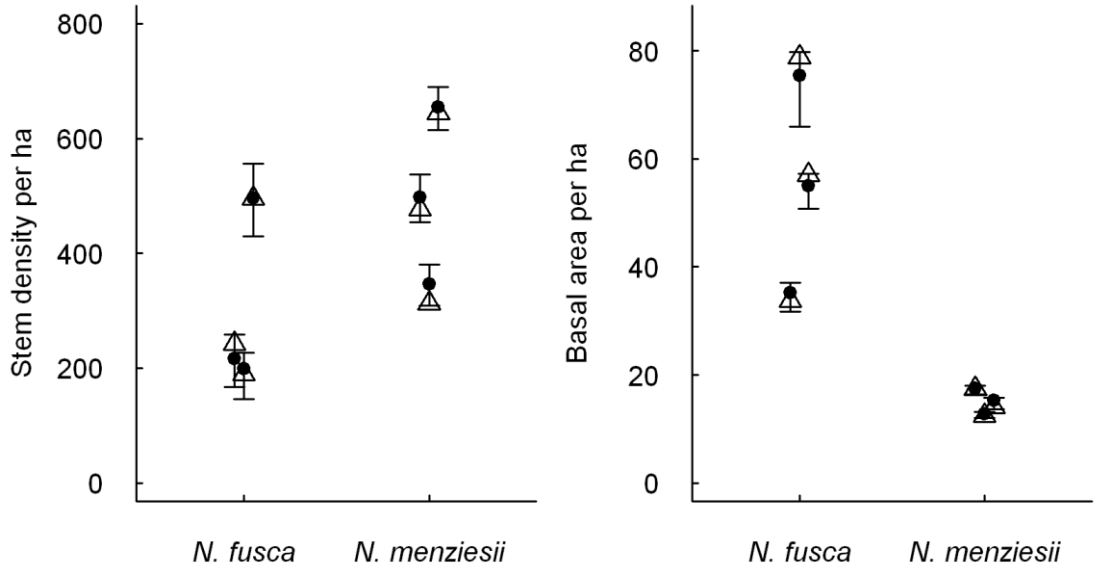

Figure 5.8. Short-term model evaluation comparing simulated vs. actual stem density and basal area over eight years. Triangles show actual stem density ha^{-1} and basal area ha^{-1} for each plot in 2009.Purple circles show simulated mean stem density ha^{-1} and basal area ha^{-1} derived from 100 simulations of the Station Creek, Rough Creek and Pell Stream permanent plots (shown consecutively left to right, for each species). Simulations ran for 8 years using data from 2001 as starting conditions. Error bars show the minimum and maximum simulated stem density and basal area across the 50 simulations.

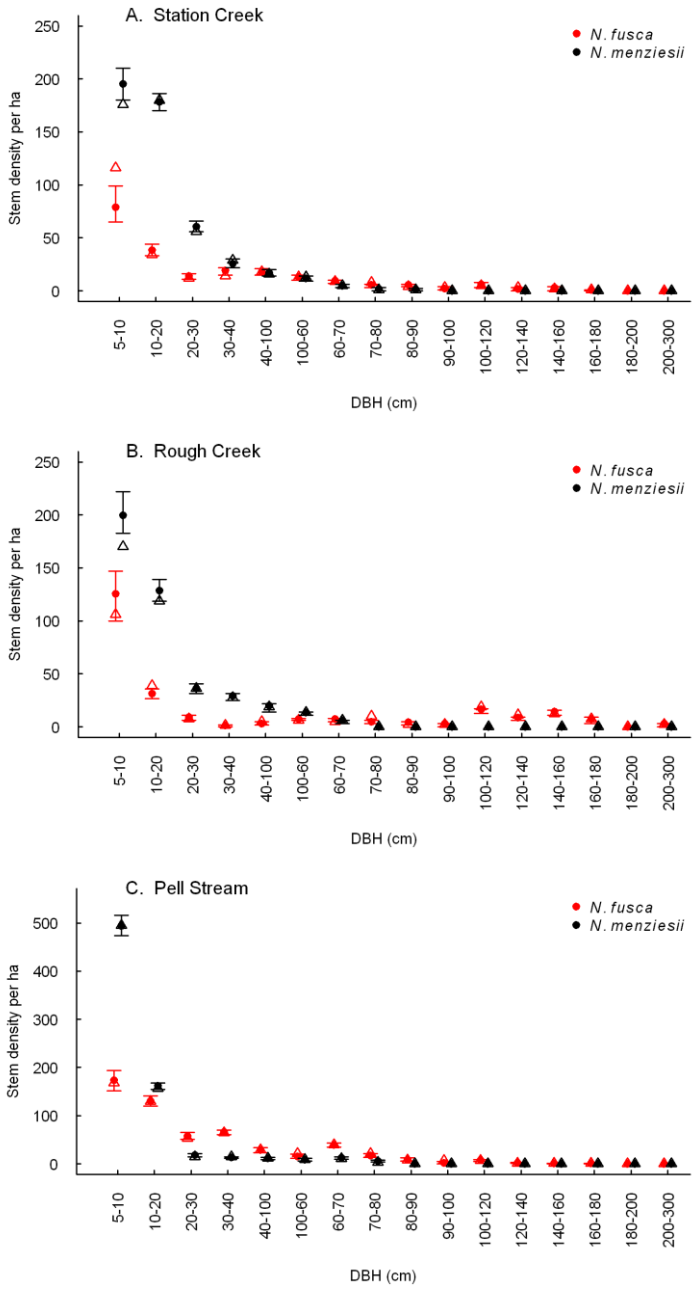

Figure 5.9. Short-term model evaluation comparing simulated versus actual size structure of *N. fusca* (red) and *N. menziesii* (purple), at A. Station creek, B. Rough Creek and C. Pell stream. Triangles show actual stem density ha^{-1} in each size class for each plot in 2009. Circles show mean simulated stem density ha^{-1} and error bars show the range (minimum and maximum) in stem density ha^{-1} for each size-class over 50 simulations run for eight years (2001–2009).

Chapter 6 Synthesis and conclusions

The main objective of this thesis was to explore the role of demographic trade-offs for forest stand dynamics of mixed-*Nothofagus* forests dominated by *N. fusca* and *N. menziesii* on the West Coast of the South Island, New Zealand. The objectives of this chapter are to: (1) synthesise the main findings of the research; (2) discuss the implications of the research findings for management of mixed-*Nothofagus* forests and (3) suggest future research direction for mixed-*Nothofagus* forests.

6.1 Performance trade-offs

In many temperate forests the regeneration success of tree species is determined by a shade-tolerance trade-off between juvenile survivorship in low light vs. growth rate in high light. Disturbance processes, that increase light availability to regenerating seedlings or saplings, are therefore considered to underpin the successional dynamics of forests and play a key role in determining forest composition. The occurrence of different patches of different ages in a forest (i.e. opened through different disturbance events through time) leads to variation in species composition and structure amongst patches, theoretically preventing the most shade-tolerant species from excluding more shade-intolerant species. At large spatial or temporal scales this general pattern is thought to allow species coexistence (Pickett and White, 1985).

Performance trade-offs at juvenile (i.e. seedling) life stages have previously been cited as the key to understanding species coexistence and forest dynamics of mixed-*Nothofagus* forests. It is therefore surprising that relatively little attention has been previously given to measuring growth and mortality rates for *N. fusca* and *N. menziesii* seedlings. Consequently, the aim of Chapter 2 was to examine seedling performance, in terms of seedling abundance, growth and mortality, for *N. fusca* and *N. menziesii* seedlings and variation in performance amongst different microsites (i.e. differing light environments and substrates). The density of naturally established seedlings varied between species, with density of *N. fusca* three-fold that of *N. menziesii*. Seedling growth rate for both species increased with total photosynthetically active radiation (PAR). *N. fusca* seedlings of all sizes grew faster on mound substrates than those on any other substrate type. The effect of substrate type on *N. fusca* seedling growth varied with seedling size: small seedlings grew faster on log substrates, but larger seedlings grew more slowly on log substrates than they did on the forest floor. For *N. menziesii*, substrate type had no effect on seedling growth. Overall, this study did not find strong evidence of a growth-mortality trade-off with respect to light, because for both species, neither light nor substrate type influenced seedling mortality rate. Mortality of *N. fusca* seedlings did, however, vary strongly with seedling size while mortality of *N. menziesii* seedlings was unrelated to seedling size.

A key finding of Chapter 2 was that different substrate types appeared to favour the ongoing growth of seedlings, compared with those that favoured seedling establishment. Given a strong previous emphasis on the importance of logs for *N. fusca* recruitment, it was surprising that *N. fusca* seedlings on logs had slower growth than

seedlings on other substrate types. This result highlights the importance of having permanently tagged individual plants to assess aspects of plant performance, such as growth and mortality, that ultimately determine recruitment rates of seedlings into larger size classes. The high abundance of very small seedlings on logs can give a misleading picture when considering the relative importance of this microsite for overall seedling recruitment.

An incomplete understanding of species coexistence and forest dynamics is provided by examining seedling subpopulations, since performance trade-off strategies of coexisting species can go beyond those observed at the regeneration phase. The seedling life stages discussed above represent just a brief snapshot in the potential life cycle of a tree so performance trade-offs at adult (i.e., canopy tree) life stages are likely to be just as important as those at seedling life stages. Establishing the nature of the competitive interactions between neighbouring adult trees and their growth and mortality rates is therefore essential for understanding forest stand dynamics. In this thesis this was achieved by analysing spatially explicit permanent plot data collected over a 23-year period that recorded the growth and mortality of individual trees.

In Chapter 3, the individual-level growth patterns of *N. fusca* and *N. menziesii* were examined across gradients of neighbourhood competition, local disturbance, and across tree sizes. Different patterns of size-specific growth were found between species: across all sizes the relatively shade intolerant *N. fusca* grew faster than *N. menziesii* on average. *N. fusca* also grew faster than *N. menziesii* at both high and low levels of neighbourhood crowding, but *N. menziesii* grew faster than *N. fusca* in recently

disturbed neighbourhoods. For both species growth was best explained by spatially-explicit neighbourhood competition indices; simpler non-spatial competition indices were uninformative. Conspecific and heterospecific neighbours were functionally equivalent in their competitive effects.

Finally, understanding rates and patterns of tree mortality is also central to understanding forest dynamics because mortality strongly influences forest structure, composition and the spatial arrangement of species and individuals. In Chapter 4 performance differences between *N. fusca* and *N. menziesii* were examined in relation to spatial patterns and rates of tree mortality. The annual mortality rate of *N. fusca* was approximately double that of *N. menziesii* (0.016 cf. 0.0089 per year). For both species, individual-based logistic models showed that slower growing trees were more likely to die than faster growing trees, but different spatial and size-related patterns of mortality were found between species. *N. fusca* trees growing in previously disturbed stands were more likely to die than those in undisturbed stands. Spatial point process analysis showed that dead *N. fusca* trees were spatially aggregated, and were segregated from living trees, a pattern that was consistent across both small and large trees. This contagious pattern of tree mortality observed for *N. fusca* is likely to be a consequence of infection by native pinhole beetles (*Platypus* spp.) larvae, which are a vector for fungal infection. Though dead *N. menziesii* were also spatially aggregated, they were not segregated from living trees, and trees in previously disturbed stands were also not subject to increased mortality.

In summary, when performance of *N. fusca* and *N. menziesii* across both the seedling and tree life stages is considered, each species appears to be favoured by small-scale disturbance processes at a different life stage, which likely contributes to their coexistence. *N. fusca* seedlings grew fast in the high light microhabitats created by small-scale disturbances, but adult tree mortality was elevated near sites of previous disturbance. By contrast, *N. menziesii* trees grew faster near sites of previous disturbance, which may help this species persist.

6.2 Sustainable management of mixed-*Nothofagus* forest

Mixed-*Nothofagus* forests hold a range of recreational, conservation, and economic values. Privately owned *Nothofagus* forest is the most common indigenous forest type managed as a timber resource in New Zealand: forests available for timber production comprise over 114 000 ha of land and the proportion of this area under government approved plans and permits is steadily increasing (Ministry of Agriculture and Forestry, 2009). New Zealand has both national and international commitments for indigenous forests to be sustainably managed (Ministry of Agriculture and Forestry, 2009). In New Zealand, controversy regarding the sustainable management of indigenous forest parallels those that face forest management elsewhere, including other southern beech forests (Lindenmayer and Franklin, 1997; Tabor et al., 2007; Pastur et al., 2009). As well as requiring timber harvest levels to be sustainable, the management systems promoted for New Zealand indigenous forests have broad objectives including

the maintenance of biodiversity and threatened species (Ministry of Agriculture and Forestry, 2009).

Management systems in New Zealand's indigenous forests come under close public scrutiny and must be seen as truly sustainable (Mason, 2000; Gillman, 2008). Previous harvest plans for Crown-owned mixed-*Nothofagus* forests were contentious, and included dispute over whether regeneration would occur in harvested areas; concern that harvesting would lead to increased mortality in residual trees and concern that models did not allow for increased risk of *Platypus* infection in harvested stands (Efford, 1999). The use of relatively simple matrix models for simulating long-term yield has also been criticised (Mason, 2000). As a result of such controversy, coupled with political considerations, silvicultural management of Crown-owned forests has ceased. However, privately-owned mixed-*Nothofagus* continue to be managed for a mix of values including timber.

Mixed-*Nothofagus* forests on privately owned land are managed using a variety of low-impact management systems, typically using patch cuts ranging in size from 0.05–0.5 ha. Experimental field trials testing the suitability of such systems are relatively uncommon in *Nothofagus* forests (Benecke and Baker, 1994; Wiser et al., 2005, 2007; Allen et al., 2012) and unlike elsewhere in the world (e.g., European forests) New Zealand forests have a very short management history and lack the long-term observational knowledge gained through decades or centuries of adaptive, region-specific, management (see Puettmann et al., 2008).

The recruitment, growth and mortality patterns of *N. fusca* and *N. menziesii* documented in this thesis provide essential baseline data to help inform sustainable management. For example, the spatially explicit individual-tree growth analyses presented in Chapter 3 included trees across a wide range of competitive neighbourhood conditions and a wide range of sizes when compared with previous studies: previous growth estimates for *N. fusca* and *N. menziesii* have typically been undertaken in forests more uniform in structure than the forest studied here, or regenerating even aged forests subject to thinning treatments or silvicultural tending (e.g., Easdale et al., 2009, 2010, 2011; but see Wiser et al., 2005; Richardson et al., 2011; Easdale et al., 2012).

Compensatory growth responses in trees growing near the edges of harvest gaps in managed forests can be significant and may determine ongoing stand dynamics and potential future yield (e.g., Jones and Thomas, 2004; Arseneault and Saunders, 2012). The present research examined tree growth in response to natural disturbances and demonstrated different patterns amongst species, with *N. menziesii* trees growing fast near sites of previous disturbance (e.g., Wiser et al., 2005). This result suggests that in managed stands, thinning operations may increase growth of *N. menziesii* across a wider range of tree sizes than has previously been considered, with potential to increase yield in such stands.

Natural disturbances in mixed-*Nothofagus* forest create heterogeneous stand conditions and appear to validate the applicability of gap-based silvicultural systems which to some degree mimic natural disturbances (Wardle, 1984). Canopy gaps created by timber harvesting may differ from natural canopy gaps, however. The tree mortality

analyses in this thesis allowed mortality processes in natural, unmanaged stands, to be compared with the results of experimental harvesting trials (e.g., Wiser et al., 2005). Though in unmanaged stands mortality of *N. fusca* appeared to be contagious, such patterns were not apparent in trees adjacent to small patch cuts (Wiser et al., 2005). This result appears to be in conflict with many studies that have shown increased tree mortality and damage due to tracking and harvesting; furthermore mortality following operational harvesting is commonly greater than that seen in experimental studies (Puettmann et al., 2008). Continued monitoring of experimental harvesting field trials described by Wiser et al. (2005) is recommended to determine whether there are time-lagged mortality responses in trees adjacent to small patch cuts, which would render patterns in the managed forest more similar to the unmanaged forest studied here. Regardless of whether harvesting leads to increased mortality in residual trees, natural disturbance processes should probably be seen as the norm and an integral part of the landscape and ecosystem dynamics of the forest, rather than as 'out of the ordinary' events (Pickett and White, 1985; Frelich, 2002; Puettmann et al., 2008).

Given the complexity of forest stand dynamics, field trials can be insufficient to assess the effects of management across relevant timescales; individual-based simulation models provide an alternative option for evaluating long-term management effects (Coates et al., 2003). Forest modeling has an especially long history in single species, even aged stands where even relatively simple, non-spatial models can be utilized (Peng, 2000). Growth and yield predictions can be made using simple relationships between stand age and timber volume, basal area and stem density (Oliver and Larson, 1990; Weiskittel et al., 2011). These simple modeling approaches are

considered most appropriate in relatively even-aged mono-specific stands (Weiskittel et al., 2011). In mixed-species all-aged stands, however, simple modeling approaches do not typically perform well, particularly as such stands tend to be structurally heterogeneous and individual tree responses to disturbance and demographic rates vary substantially amongst life stages and across species.

In Chapter 5, a spatially explicit simulation model for tree population dynamics is described which was parameterised specifically for mixed-*Nothofagus* forest using data on the recruitment, growth and mortality of individual trees. The model was used to explore the consequences of disturbances of varying frequency on long term trends in forest structure and composition. This included evaluating the potential long term effects on forest composition and structure of two alternate harvesting regimes for mixed-*Nothofagus* forest. Simulation results showed that the frequency of small-scale disturbance was a major determinant of forest composition and structure after 500 years, determining whether conditions favoured dominance of *N. fusca* or *N. menziesii*. Across the 500-year simulated timeframe, harvesting had minimal or unrecognizable effects on overall structure and composition, provided each harvest operation only occurred after forest had recovered from previous harvests. More frequent harvesting (i.e., 10% of stand biomass every ten years) resulted in forest dominated by small *N. fusca* and a likely deterioration of a variety of natural values that are dependent on maintaining a larger range of tree sizes (Norton, 1996).

It may also be useful to consider the impacts of harvesting in relation to long-term successional pathways operating in these forests. It was notable, for example, that all

simulation runs (i.e. both including and excluding harvesting) led to forest with fewer large trees compared with the initial stands. In many forests large trees comprise a high proportion of forest wood volume, biomass and carbon. Large *Nothofagus* trees provide important habitat for some New Zealand bird and invertebrate species (Wardle, 1984, Norton, 1996). Any decline in large trees abundance, whether occurring through management operations or natural stand dynamics, may therefore be of considerable concern (e.g., Lindenmayer et al., 2012). The reason for the loss of large trees, in all simulation runs, is unknown. The synchronous dieback and death of large trees may be a legacy of a previous extensive catastrophic disturbance (such as a major seismic event), which initiated a cohort of similarly aged trees that are now senescent. A formal sensitivity analysis of the simulation runs is now required, to examine how sensitive the simulation outcomes are to large-diameter tree mortality rates.

Finally, the management of mixed-*Nothofagus* forests must also be economically feasible, which may require an expansion of current markets for *Nothofagus* timber. Management of mixed-*Nothofagus* forests on public lands will also only be politically feasible if there is greater public acceptance of management of indigenous forests.

6.3 Research needs for mixed-*Nothofagus* forest

Two main avenues of further research logically flow-on from this thesis that would help further inform the sustainable management of mixed-*Nothofagus* forest. First, it is important to consider whether the demographic patterns described in this thesis are also general to mixed-*Nothofagus* forest across a broader geographic area. It must be acknowledged that the present research was conducted on relatively homogenous terrace sites within a relatively small geographical area. Many previous studies have shown that the recruitment, growth and mortality of trees can vary along edaphic or climatic gradients (e.g., Canham et al., 2006; Getzin et al., 2008; Coates et al., 2009; Easdale et al., 2012). The nature of competitive interactions between neighbouring trees can also vary with such factors, as a consequence of shifts in the relative importance of above and below-ground competition, or even the occurrence of positive interactions between neighbouring trees (Bertness and Callaway, 1994; Maestre et al., 2009). Therefore, the generality of the results presented in this thesis to mixed-*Nothofagus* forest over a wider geographic area is unclear. Future studies should examine variation in recruitment, growth or mortality across edaphic and climatic gradients.

Second, it is important to consider whether the dynamics of unmanaged mixed-*Nothofagus* forest are directly comparable with managed mixed-*Nothofagus* forest. When it comes to forest management, examination of the dynamics of unmanaged forest is necessitated by the paucity of long-term research trials in managed forest. In managed mixed-*Nothofagus* forest, management impacts have previously only been

assessed over short timeframes compared with the entire management cycle. An unresolved issue is whether residual tree mortality surrounding harvest gaps will be elevated, compared with 'background' mortality rates. Monitoring of the impacts on residual trees of small harvest gaps has so far suggested that mortality is not elevated over the first decade following harvesting (Wiser et al., 2005) however this result is in conflict with the mortality patterns found in unmanaged forest presented in this thesis, where mortality rates of *N. fusca* were elevated near natural canopy gaps. Given that harvest gaps differ from natural canopy gaps in a number of ways, this issue should be resolved through ongoing monitoring of tree harvest field trials.

Future research on mixed-*Nothofagus* forest dynamics will be reliant on the establishment and maintenance of long-term permanent plot datasets. Much prior research has been undertaken on mixed-*Nothofagus* forest dynamics, though studies in the past have mainly relied on shorter term data, stand reconstruction or dendrochronological techniques, or one-off observational surveys (Stewart and Rose, 1990; Runkle et al., 1995; Runkle et al., 1997; Vittoz et al., 2001; Wiser et al., 2005; Wiser et al., 2007). One-off surveys (e.g., dendrochronology studies to examine tree growth rates) likely bias the estimation of tree growth rates (e.g., where only a surviving subpopulation of trees is sampled) and are also unable to relate tree mortality to tree growth. Permanent plots that follow the fates of the entire population of trees provide a much more comprehensive insight into forest stand dynamics. The establishment and maintenance of permanent plots should also be a requirement in managed forests and the collection of site-specific data would ensure that harvest rates can be set at sustainable levels. Most plot datasets (such as used in this thesis) are short relative to

the potential life span of *Nothofagus* trees and plots are seldom large enough to capture the influences of tree neighbourhoods on growth or mortality rates (for example, most permanent plots in New Zealand are only 20 × 20 m in size). Therefore, continued monitoring of the large (0.8–1 ha) permanent plots studied here should be undertaken.

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